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Measurement and Inheritance of Resistance to Sheath Blight Caused by *Rhizoctonia Solani* Kuhn in Rice.

Xueyan Sha

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MEASUREMENT AND INHERITANCE OF RESISTANCE TO SHEATH BLIGHT
CAUSED BY *RHIZOCTONIA SOLANI* KÜHN IN RICE

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Plant Pathology and Crop Physiology

by

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ABSTRACT

Sheath blight (ShB), caused by *Rhizoctonia solani* Kühn, has been the most destructive rice disease in Louisiana. To breed ShB resistant varieties, an effective procedure for screening progenies of segregating populations is required and detailed knowledge of the mode-of-inheritance of partial ShB resistance is also needed.

In this study, four inoculation methods: rice hull/grain mixture (MIX), rice straw, toothpick, and brown rice, along with five assessment systems: 0-9 rating scale (RAT9), relative lesion height (RLH), disease severity (DS), disease incidence, and lesion height were compared on nine rice genotypes showing different resistance levels to ShB. Progenies of segregating populations from crosses between the ShB resistant rice genotypes H₄/CODF, LB86-30344, Jasmine 85, Teqing, Gui Chao, and Yangdao 4 and the susceptible cultivar Lemont and crosses among the resistant genotypes were field screened for ShB resistance using the highly virulent *R. solani* isolate LR172 from 1995 to 1997.

The best separation between rice genotypes with different levels of partial ShB resistance was obtained by the MIX method of inoculation and the RAT9, RLH, and DS assessment systems. Inheritance studies showed that H₄/CODF, LB86-30344, and Jasmine 85 had a common dominant gene designated as *Rh-2* for partial ShB resistance, which was nonallelic to the common dominant gene *Rh-3* in Teqing and Gui Chao. Both *Rh-2* and *Rh-3* were inherited independently from the recessive gene *rh-1* in LSBR-5. The broad-sense heritabilities estimated from F₃ and F_{2,4} lines from the

Jasmine 85 x Lemont and LB86-30344 x Lemont crosses ranged from 73.2% to 82.1%.

Two of three undesirable agronomic traits, tall plants, pubescent foliage, and red pericarp, found in the partial resistance sources LB86-30344 and H₄/CODF, were monogenically inherited and inherited independently from the *Rh-2* gene, but *Rh-2* was loosely linked to the gene for red pericarp with a crossover value of 0.45. The *Rh-2* and *Rh-3* genes appeared to have an additive effect for partial ShB resistance when combined in the same breeding lines.

CHAPTER 1. REVIEW OF LITERATURE

1.1. INTRODUCTION

Rice sheath blight (ShB), caused by the fungus *Rhizoctonia solani* Kühn, is regarded as an internationally important disease of rice (*Oryza sativa* L.) which is second among fungal diseases only to rice blast in potential for yield loss (Ou, 1985). Miyake first reported this disease in Japan in 1910. Since then, this disease has been recorded in almost all rice growing areas in south and southeast Asia (Ou, 1985; Dasgupta, 1992). In the United States, Ryker and Gooch (1938) first reported the bordered sheath spot disease which has symptoms very similar to ShB. ShB has also been reported from Brazil, Colombia, Surinam, Venezuela, and Madagascar and is considered to occur worldwide where rice is grown (Ou, 1985; Rao, 1995).

Sheath blight has become one of the most important rice diseases in the past 25 years because of the adoption of new semidwarf rice cultivars and the increased application of nitrogen fertilizers, resulting in thicker stands and higher humidity inside the rice canopy (Xie et al., 1990). In southern rice growing areas of the United States, rotation with soybean (*Glycine max* L.), another host for *R. solani*, contributed to the dramatic increase of ShB incidence (Lee and Rush, 1983).

Symptoms of ShB include spots on leaf sheaths, leaf blades, and panicles of rice plants. Susceptible plants may be severely blighted under conditions favorable for disease development. This leads to incomplete filling of the grain, which lowers grain yield and milling quality. In addition, ShB weakens the culm making the plant more susceptible to lodging (Dath, 1990).

It is very difficult to control ShB using cultural practices (Lee and Rush, 1983). Chemical control is effective, but it is expensive and causes potential environmental concerns. Therefore, breeding and utilization of resistant cultivars is the only practical and economic way to control this disease.

To date, no complete ShB resistance has been identified in rice throughout the world. Only moderate or partial resistance is available (Dasgupta, 1992). A few genetic studies have been conducted using moderately or partially resistant cultivars. The results were fragmentary and controversial. In 1951, Hashioka reported that ShB resistance was controlled by one major dominant gene. Later, several reports suggested that ShB resistance in United States long-grain cultivars was conferred by one or two completely or partially dominant genes (Masajo, 1976; Goita, 1985; Hoff et al., 1984; Hoff et al., 1985). Recently, two elite ShB resistant lines were developed through somaculture (Xie et al., 1990, 1992). The resistance in these lines was conferred by one or two recessive genes. Some positive progress has been made in breeding resistant cultivars using those somaclonal variants (Rush et al., 1995; Rush et al., 1996). However, many researchers attribute moderate or partial ShB resistance to such characters as late maturity and plant height (Hashiba et al., 1982). After analysis of the ShB resistance of several indica cultivars including Tetep, IET4699, Retna, and Kataktara Da2, it was reported that the resistance of these cultivars was polygenically inherited (Zhu et al., 1990). However, these fragmentary results do not satisfactorily explain the inheritance of ShB resistance in rice.

1.2. THE FUNGUS

1.2.1. NOMENCLATURE

Rice ShB is caused by the fungus *Rhizoctonia solani* Kühn [teleomorph: *Thanatephorus cucumeris* (Frank) Donk]. Historically, this fungus has been described with several synonyms such as *Sclerotium irregulare* Miyake, *Hypochues sasakii* Shirai, *Corticium vagum* Bert & Cart., *Corticium solani* (Prill & Delancy) Bourd and Galz, and *Pellicularia filamentosa* (Pat.) Rogers f. sp. *sasakii* (Peng et al., 1986; Rao, 1995). The teleomorph of *R. solani* belongs to the subdivision Basidiomycotina and the class Hymenomycetes (subclass Holobasidiomycetidae). The current species concept stipulates that isolates of *R. solani* possess the following characteristics: a) some shade of brown hyphal pigmentation, b) branching near the distal septum of cells in young vegetative hyphae, c) construction of hyphae and formation of septa, d) dolipore septa, and e) multinucleate cells in young vegetative hyphae. Characteristics, such as monilioid cells, sclerotia, hyphae greater than 5 µm in diameter, rapid growth rate and pathogenicity are usually present, but they may be lacking in some isolates. Morphological features that are never present include: clamp connections, conidia, sclerotia differentiated into rind and medulla, rhizomorphs, and pigments other than brown (Sneh et al., 1991).

Moore (1987) indicated that the anamorphs of the form genus *Rhizoctonia* are heterogeneous. The type species, *Rhizoctonia crocorum* (Pers.) DC: Fr., is the anamorph of *Helicobasidium brebisonii* (Desm.) Donk. The simple pored basidiomycete-type septum, which is distinct from that of doliporous species having a distinct 5S ribosomal RNA sequence, indicates that *R. crocorum* is an ustomycete. He placed the anamorphs

of *Thanatephorus* spp. in *Moniliopsis* Ruhland, reserving the genus *Rhizoctonia* for anamorphs of ustomycetous fungi which have septa with simple pores. However, it can be argued that given the extensive literature on *R. solani*, and the familiarity of plant pathologists with the name *R. solani*, a name change may create more chaos than necessary (Sneh et al., 1991).

1.2.2. ANASTOMOSIS GROUPS

Based on affinities for hyphal fusion (anastomosis), *R. solani* can be placed in one of ten anastomosis groups (AGs), all represented by the same teleomorph. Each AG represents a noninterbreeding population and a genetically independent entity. Again, based on pathogenic, morphological, and physiological characteristics and DNA homology, intraspecific groups (ISGs) have also been recognized within these ten AGs. The ShB fungus was placed in AG-1, which can be further divided into three ISGs, AG-1-IA, AG-1-IB, and AG-1-IC based on sclerotial form, cultural characteristics, and DNA base sequence homology (Sneh et al., 1991). AG-1-IA isolates cause typical rice ShB. Web blight isolates, AG-1-IB, produce different symptoms on rice, and the sugar beet and buckwheat isolates, AG-1-IC fuse well with IA and IB, but are not pathogenic to rice (Sneh et al., 1991; Rao, 1995). A test conducted by O'Neill et al. (1977) indicated that the *R. solani* isolates causing ShB of rice in Louisiana belong to AG-1.

1.2.3. HOST RANGE

The ShB fungus has a wide host range and can infect plants belonging to 43 families and 263 species (Peng et al., 1986). Bandara and Nadaraja (1979) found that two virulent isolates of *R. solani* can infect and survive on several weeds common in rice

fields. The symptoms on *Echinochloa colonum* (Linn) Link, *Echinochloa crusgalli* (Linn) L. P. Beauv, and *Fimbristylis littoralis* Gaud. are similar to those on rice plants. Two other *Oryza* species, *O. australiensis* Domin and *O. nivara* Sharma and Shastry, are highly susceptible to the disease, whereas several entries of *O. rufipogon* Griff., *O. barthii* A. Chev., and *O. minuta* J. S. Presl ex C. B. Presl were resistant (Nayak et al., 1979). Mew et al. (1980a and 1980b) listed graminaceous weed hosts and also showed that the isolates from weed grasses were highly virulent to rice.

1.2.4. PATHOGENIC VARIATION

Sources of ShB resistance identified in one region may not perform with the same degree of resistance in other regions, indicating pathogenic variability of the fungus. Considerable variation in the degree of aggressiveness among different isolates of the fungus was observed in China. Guo et al. (1985) reported three types of pathogenic variation among 47 isolates of *R. solani* collected from different rice growing areas based on testing with three differential rice cultivars. In India, Nandi and Chakrabarti (1984) inoculated 10 rice cultivars with seven isolates of *R. solani* from different locations in the eastern and northeastern regions of India. Significant cultivar by isolate interactions were detected. Based on the reaction of the 10 cultivars, those seven isolates can be grouped into four pathotypes. Recently, Pillai and Singh (1994) tested seven Indian isolates on 23 rice genotypes. The results showed different degrees of aggressiveness among different isolates in repeated tests under field and laboratory conditions. These seven isolates were grouped into six pathotypes according to their virulence on the tested cultivars.

In Louisiana, it was found that all *R. solani* isolates in AG-1 from rice, soybean, sorghum, and weed grasses were nearly identical in cultural characters. Greenhouse tests showed that, in general, the virulence of single basidiospore isolates of *R. solani* was very low. However, the varietal reaction to single basidiospore isolates was highly correlated with the varietal reaction to field isolates (O'Neill, 1976, O'Neill and Rush, 1982).

After extensive study of pathogenic *R. solani* isolates from rice-based agricultural systems in southeast Asia and West Africa, Banniza et al. (1996) reported that the majority of isolates belonged to AG-1 and were highly variable morphologically with no consistent characters that related to the host of origin, production system, or geographic region. Pathogenicity testing on rice, soybean, and a range of weed species indicated that these strains showed little host specificity.

1.3. DISEASE DEVELOPMENT AND LOSS

1.3.1. SYMPTOMS AND SIGNS

Rhizoctonia solani causes spots on the leaf sheath. The spots are at first ellipsoid or ovoid, somewhat irregular, greenish-grey, varying from 1 to 3 cm long. The center of the spot becomes grayish-white, with a brown margin. Sclerotia are formed on or near these spots. The size and color of spots and the formation of sclerotia depend on environmental conditions. The pathogen is primarily soil-borne, but occasionally seed-borne when the infection reaches panicles or when basidiospores initiate infection (Ou, 1985). Outer leaf sheaths are first affected, gradually extending towards the inner sheaths. Sheath blight lesions spread more rapidly on the leaf blade than on the leaf

sheath. Lesion length increases faster at heading than at booting and maximum tillering stages (Lee and Rush, 1983). At booting, the development is more rapid on the lower leaf sheaths than the upper leaf sheaths, but the reverse is true at heading. In addition, ShB weakens the culm making the plant more susceptible to lodging (Masajo, 1976). Sclerotia, initially white but turning brown at maturity, are produced superficially on or near the infected tissue after about 6 days. Sclerotia are loosely attached and easily dislodged from the plant at maturity (Dath, 1990).

1.3.2. DISEASE CYCLE

Sclerotia and, to a lesser degree, mycelia in plant debris are the means of pathogen survival between crops and are the primary inoculum (Lee and Rush, 1983; Damicone et al., 1993). The sclerotia are easily detachable from the host and remain viable in soil for several months over a wide range of temperature and moisture conditions (Rao, 1995). After transplanting or on seedlings produced by direct seedling, the sclerotia floating on the surface of the water contact the surface of the sheath of rice plants where they germinate and initiate infection. The fungus produces two types of mycelia, the straight runner type and the lobate type. The straight runner mycelium grows on the surface of plant tissues but does not produce any lesions. The lobate type infects the tissue and produces lesions (Ou, 1985). Close observations on the infection processes involved in the disease were carried out by several researchers (Hashioka and Okuda, 1971; Marshall and Rush, 1980a and b; Matura, 1986; Kim et al., 1990). Prior to infection, the organism forms two types of structures, the lobate appressorium and the infection cushion. Infection takes place by cuticular penetration or through the stomata.

One or few infection pegs are formed from each lobe of the lobate appressorium and are produced more commonly than those from infection cushions. Stomatal invasion seldom occurs on the outer surface of the sheath, but is quite common on the inner surface.

Soon after the primary lesions are formed, mycelium grows rapidly on the surface of the plant and inside its tissues, proceeding upwards as well as laterally and initiating secondary lesions. Even though basidiospores may form on leaves near the infected tissues under conditions of extremely high humidity, they play a minor role in ShB development in rice. The mycelium from the infected rice plant is the main source of inoculum for ShB spread from plant to plant (Gangopadhyay, 1983). When the ShB fungus is not actively colonizing a host, it mainly survives in the form of dormant structure of sclerotia which will stay alive over the winter and will initiate the primary infection next season (Dath, 1990).

1.3.3. EFFECTS OF ENVIRONMENTAL FACTORS

Infection may occur at temperatures ranging from 23-35°C, with the optimum 30-32°C. High relative humidity, typically 96-97%, is required. Endo (1930) reported that at 32°C, infection took place in 18 hours, and at 28°C in 24 hours, with continuous wetting.

While the temperature within the rice crop varies with that of the air temperature, humidity among the plants is greatly affected by the thickness of the stand. Close planting of semidwarf cultivars and heavy applications of fertilizers, leading to thick growth, tend to increase disease incidence. This explains why ShB is usually observed in the field after the plants have reached the maximum tillering stage, when canopy closure

allows the maintenance of high humidity conditions (Ou, 1985). Hashiba (1985) studied the effects of different temperatures and relative humidities on the vertical spread of ShB. The results indicated that under 100% relative humidity (RH), the vertical development rate of ShB was 1.30 cm per day at 23°C, 1.35 cm per day at 25°C, and 1.58 cm per day at 28°C. The vertical spread at 25°C was 0.99 cm per day at 98% RH, 0.97 per day at 96% RH, 0.87 per day at 90% RH, and 0.38 per day at 86% RH. Shi and Cheng (1995) found that in China the high temperatures during May and June resulted in an increase in disease index, but high temperatures in July inhibited disease development.

There are numerous reports of increased disease severity associated with increased use of nitrogen fertilizer (Ou, 1985; Lee and Rush, 1983; Cu et al., 1996). Direct changes in the host's susceptibility with high nitrogen supply have been postulated. Kozaka (1961) reported that the susceptibility of the leaf sheath is closely correlated with its nitrogen content, but not with its content of sugar or starch. Savary et al. (1995) studied the direct and indirect effects of nitrogen supply on ShB development. They found that increased nitrogen supply increased host plant tissue contacts (blade to blade and blade to sheath), increased the capacity of the canopy to retain moisture, and increased the leaf nitrogen content. Multiple regression and path coefficient analysis suggested that nitrogen drives focal expansion in ShB essentially via indirect effects: increased tissue contacts in the canopy and higher leaf wetness.

1.3.4. YIELD LOSS

Kozaka (1970) reported a yield loss of 25% when ShB extended up to the flag leaf, and a 30-40% yield loss when severe infection of leaf sheath and leaf blades

occurred. IRRI (1975) reported yield losses as great as 24% in susceptible rice cultivars under the highest levels of disease intensity and nitrogen application. In Texas, Marchetti and Bollich (1991) reported a mean yield loss of 40.9% when the mean ShB severity was 7.6 on the 0-9 rating scale (maximum is 9).

Several linear models were developed to estimate yield loss under experimental conditions. Ahn et al. (1986) found a close correlation between relative lesion height (RLH) and yield under moderate disease pressure. No significant yield loss was observed when RLH was less than 20%, however, a 46% yield loss resulted when RLH equaled 90%. Hashiba et al. (1983) developed a linear function to estimate the yield loss caused by *R. solani* based on both RLH and percentage of affected hills.

$$L = (41.31 X - 826.2) \times A/1000 \text{ kilogram}$$

Where L = yield loss per 10 acres, X = ratio of uppermost lesion height to the plant height, and A = percentage of affected hills. This model was verified by 4 years of field data. Based on this model, the first computerized forecasting software BLIGHTAS was developed (Hashiba and Ijiri, 1989).

Rice growth stage has a large effect on ShB development and yield loss. Yield loss due to ShB may occur at any stage, but is higher when infection occurs at booting or flowering (Sharma et al., 1990b, 1994; Vanitha et al., 1996).

1.4. DISEASE CONTROL

1.4.1. CULTURAL CONTROL

Because the primary inoculum level is the key factor in epidemics of ShB, management or elimination of sclerotia and mycelia from rice fields should be effective in

controlling this disease (Yamaguchi et al., 1971). However, sanitation and other cultural practices rely heavily on the specific rice-growing agroecosystem. Burning of rice straw can not eliminate sclerotia in the soil. Because of the labor cost, removal of floating sclerotia from rice fields before transplanting might be effective in developing countries, but could not be adopted by developed countries. Crop rotation has not been as successful in controlling ShB as for other diseases, due to the broad host range and long viability of propagules of the fungus. Planting green manure crops such as *Sesbania aculeata* Pers., *Crotalaria juncea* L., and *Cicer arietinum* L. was reported to be effective in reducing the viability of the sclerotia in soil (Dath, 1990).

1.4.2. BIOLOGICAL CONTROL

Endo et al. (1973) suggested the possible use of *Neurospora crassa* Shear et Dodge to control ShB of rice. Incidence of *R. solani* was markedly reduced by *N. crassa* in the soil, while seedling growth was unaffected.

Devi et al. (1991) found that strains of both fluorescent and non-fluorescent *Pseudomonas fluorescens* Migula isolated from rice rhizospheres in south India inhibited mycelial growth and affected sclerotial viability *in vitro*. In field tests, IR50 and TKM9 rice plants grown from bacteria-treated seeds had 65-72% less ShB than those plants grown from untreated seeds. Several enterobacteria, *Bacillus subtilis* Cohn, *B. pumilus* Meyer and Gottheil, and *B. laterosporus* Laubach also reduced the viability of sclerotia in the soil (IRRI, 1988).

Various fungi, such as *Gliocladium virens* Miller, Giddens and Foster, *Trichoderma viride* Pers., *T. harzianum* Rifai, *T. aureoviride* Rifai, *T. pseudokoningii*

Rifai, *Aspergillus niger* van Tieghem, *A. terreus* Thom, and *Penicillium* spp. have been isolated from soil, sclerotia of *R. solani*, and healthy or infected plant parts. They can inhibit mycelial growth, suppress formation and germination of sclerotia, and cause lysis due to hyperparasitism (Manibhushanrao et al., 1989). *Trichoderma harzianum* releases extracellular chitinase, β -1,3-D-glucanase and degrades the *R. solani* cell wall (Sreenivasaprasad and Manibhushanrao, 1990). Soil inhabiting *Trichoderma* spp. can colonize and kill the sclerotia on infected rice stubble under conditions of high humidity (Mew et al., 1980). Among the many potentially antagonistic soil fungi, *Gliocladium* and *Trichoderma* spp. have been used as biocontrol agents for *R. solani*, as they have been termed presumptive mycoparasites (Rosales and Mew, 1982; Manibhushanrao et al., 1989). In studies with two *Trichoderma longbrachiatum* Rifai and three *G. virens* isolates, Manibhushanrao et al. (1989) observed that these two species also possess antibiotic activity apart from mycoparasitic activity which can be detected by the application of cycloheximide, a protein synthesis inhibitor. After treatment with 10 ppm cycloheximide, these isolates lost the ability to colonize the pathogen. However, the practice of biological control is not well established, and the effective commercial application of such control measures against rice ShB has not been reported.

1.4.3. CHEMICAL CONTROL

Control of ShB with fungicides has been used for many years in Japan and other countries (Ou, 1985; Rush and Lindberg, 1972, 1974; Rush et al. 1983; Rush et al. 1984). In recent years, the total area treated with chemicals for the control of ShB in Japan has reached 1.7 million hectares. Korea alone utilizes 2-3 million kilograms of

fungicides to control ShB every year (Rao, 1995). Since the early 1970s, benomyl (Benlate) has been widely tested around the world and found effective for ShB control (Chien and Chu, 1973; Rush et al., 1976, 1984; Jones et al., 1987; Kataria et al., 1991). Besides benomyl, iprodione (Rovral), propiconazole (Tilt), and flutolanil (Moncut) also were found to be effective against ShB (Van Eeckhout et al., 1991; Jones et al., 1987; Groth and Rush, 1988). Several antibiotics from *Streptomyces hygroscopicus* var. *limoneus* Nov. were developed in Japan and China and have proven to be very effective against ShB. Validacin-A (3% liquid/0.3% dust) earned an extremely favorable reputation all over the world and was registered as an effective control agent for ShB (Furuta, 1973; Endo et al., 1983). Jinggangmycin developed in China has been highly effective against ShB and other fungal diseases. Ninety percent protection can be achieved with the application of only 50-75 grams of active compound per hectare (Peng et al., 1986).

1.5. HOST RESISTANCE

1.5.1. INOCULATION METHODS

Because soilborne sclerotia serve as primary inoculum and secondary infection relies heavily on hyphal spread from plant to plant, the disease does not occur uniformly in the rice field. Artificial inoculation is necessary to test rice plants for ShB resistance. Yoshimura and Nishizawa first compared various methods for testing for resistance in 1954. They found: (1) field tests using artificial inoculation increased efficiency and the uniformity of infection; (2) seedling tests showed no differences in percentage of diseased tillers; (3) maximum tillering is the optimum growth stage for cultivar testing;

and (4) straw culture (rice straw infested with *R. solani*) inserted among tillers of each hill and evaluated after two months worked well in irrigated fields. Disease in these studies was measured by the disease index, calculated by the following formula:

$$\text{Disease Index} = \frac{3n_1 + 2n_2 + 1n_3 + 0n_4}{3N} \times 100$$

Where N = total number of tillers in a plant; n_1 = number of tillers having infection on the upper four sheaths and leaf blades including the flag leaf and its sheath; n_2 = number of tillers have infection on three sheaths and leaf blades below the flag leaf; n_3 = number of tillers having infection on third and fourth sheaths and leaf blades below the flag leaf; and n_4 = number of healthy tillers.

The International Rice Research Institute (IRRI, 1973) developed the following inoculation methods: (1) Insertion of a single sclerotium into the leaf sheath of two tillers per hill. (2) Three pieces of straw cultures infested with *R. solani* about 8-10 cm long were placed among the tillers of a hill and the entire hill was wrapped with paper that touches the irrigation water. (3) Detached flag leaves were inoculated by using monosporal culture of basidiospores. (4) Seedling inoculation was done at 20-25 days after planting following the toothpick method. (5) Adult plant inoculation was made either by sclerotial insertion or by hyphal tip insertion. Disease index was calculated on the basis of percentage of infected area on each leaf sheath from three representative tillers from each hill. A Standard Evaluation System (SES) 0-9 scale also was used to rate the ShB reactions (IRRI, 1980).

Amin (1975) developed the Stem-Tape-Inoculation method. The fungus was grown on potato sucrose agar or autoclaved rice stem pieces. Two to three such pieces were placed directly into noninjured sheaths of 6-week-old rice plants either grown in the greenhouse or field. The inoculum was placed about 6-10 cm above the water line and covered with masking or cellophane tape. Inoculated plants were kept in humidity chambers for 6 hours per day for 3 days after inoculation when grown in the greenhouse. In the case of field inoculation, the plants were sprinkled with water for 4 hours per day after inoculation. Scoring was done using a SES 0-9 scale. Chakrabarti (1979) suggested that this technique may be particularly suited to low-humidity areas.

A syringe inoculation method was developed by Wasano et al. (1982). A *R. solani* isolate was cultured on potato dextrose agar (PDA) medium at 28°C for 2 days. A 0.25 ml aliquot of crushed mycelia was injected into the third leaf sheath interstice at the heading stage. The resistance level of each tested plant was scored on the second leaf sheath 4 weeks after inoculation, based on the ratio of the area of the diseased lesion to that of the total leaf sheath. This method was found to be the most efficient and reliable when compared with three other methods: pieces of rice straw, rice grain/hull mixture, and fungal disks.

The rice grain/hull mixture method developed by Dr. Rush has been a common method to test large numbers of rice plants under field conditions (Rush et al., 1973). The *R. solani* infested mixture was hand-distributed over the rice plants of a test plot. To prepare the inoculum, rice grain and hulls were mixed (1 part grain to 2 parts hulls by volume) and then placed in autoclave bags. Water was then added to the bags in a ratio

of 1 part water to 2 parts mixture on a volume basis. The bags were autoclaved on two consecutive days at 121°C for 45 minutes each time. The autoclaved mixture was laid in a thin layer (about 3-5 cm deep) on a table covered with a sheet of clear plastic film. Plugs from five-day old cultures of *R. solani* growing on PDA were incorporated into the mixture. The inoculated mixture was cultured at room temperature for three days. Rice plants in a 2.1 meter row were inoculated with 25 ml of this inoculum mixture at the maximum tillering stage. The disease reaction was rated 30 days after heading based on a 0-9 rating scale (Rush et al., 1973, 1976). Masajo (1976) compared the rice grain/hull mixture method and string method, and found that the rice grain/hull mixture method was easy to apply and effectively differentiated among genotypes with different levels of ShB resistance.

Sharma et al. (1990a) compared disease development resulting from inoculation with mycelia, rice grain/hull mixture, sclerotia, and naturally infected rice stems. Infected rice stem inoculum differed significantly from the other inoculum sources and produced the lowest area under the disease progress curve (AUDPC). The three other inoculum sources were equally effective for inciting ShB development under greenhouse conditions.

All rice plant foliage, including the leaf blade, leaf sheath, and panicle, can be infected by *R. solani*. This makes the accurate evaluation of ShB very difficult. An efficient assessment method is the key to identify individual resistant genotypes among a segregating rice population. Five assessment methods, highest relative lesion height (HRLH, %), disease severity (DS, %), disease incidence (DI, %), SES (0-9 scale), and

real area infected (RAI, %) were evaluated on three rice cultivars at IRRI (Sharma et al., 1990c). HRLH and DS were considered the most convenient and dependable assessment methods. They are easy to use and accurately discriminate among cultivars. The DI and SES methods were not recommended because they do not give an accurate assessment or a quantitative measure of real infection, respectively. The 0-9 rating scale proposed by Dr. Rush has been widely used and has been proven to be more effective in discriminating ShB resistance among rice genotypes than 0-5 rating scale (Rush et al., 1976; Jeutong, 1985). A reduced number of infection cushions produced by *R. solani* and a dark zone around smaller lesions were also suggested as effective methods to select for ShB resistance (Groth and Nowick, 1992; Dath, 1985).

Even though a large number of ShB inoculation methods and disease assessment systems were developed, most of these methods were designed to test homozygous rice cultivars or germplasms, and some were only effective in seedling tests or greenhouse tests (Masajo, 1976; Jeutong, 1985; Amin, 1975). Large differences in ShB reaction were observed between seedling and field tests using the same rice cultivars (Masajo, 1976; Guo et al., 1985). Different inoculation methods and evaluation systems were adopted by different researchers to study the inheritance of ShB resistance. This may contribute to the controversies surrounding the mode-of-inheritance of resistance to this disease (Hashioka, 1951a and b; Sha and Zhu, 1989, 1994; Goita, 1985; Jeutong, 1985). It is necessary to evaluate inoculation and assessment methods and select a suitable system to discriminate among phenotypes in segregating populations under field conditions for determining the inheritance of ShB resistance.

1.5.2. CULTIVAR REACTIONS

After extensive screening of rice germplasm and relative wild species, no immunity or complete ShB resistance has been reported. However, the existence of moderate or partial resistance was confirmed by different researchers in several countries.

In India, Rao et al. (1989) tested 38 rice cultivars for ShB resistance in the field in 1986-87. The cultivars RNR 6250, RNR 74802, and RNR 1535 had the least infection in both years. Panda (1989) tested 91 rice cultivars under natural infection by *R. solani*. None of them showed immunity, but 14 were resistant and 28 were moderately resistant, the remainder being moderately to highly susceptible. Ansari et al. (1989) screened 267 rice genotypes for ShB resistance in the laboratory. Twenty were found to be resistant including IET 7918, Bog II, and Aduthurui. Singh and Dodan (1995) tested 73 promising genotypes and found that IR40 and KK2 exhibited resistance to ShB both in laboratory and field tests.

In China, Sha and Zhu (1989) tested 13 rice cultivars with different levels of partial resistance in the field during 1985-87. Tetep, Ta-poo-cho-z, and Guyanal were found to be consistently resistant. Kim et al. (1990) studied the varietal resistance to ShB in rice in Korea. Nineteen cultivars showed moderate resistance to multiple *R. solani* isolates. Based on their reactions to different isolates, those cultivars were divided into two groups. At IRRI, 7614 entries were tested against *R. solani* in different locations around the world (mainly in Asia) and over different seasons. Seventy-two entries were

identified as resistant, of which 48 were upland genotypes, 17 were wild rice accessions, and only three were elite lines (Rao, 1995).

In Japan, Kozaka (1961) found no significant difference in reaction to ShB among cultivars tested when they were 40-50 days old. Early maturing cultivars appeared to suffer more than late maturing ones, because the later cultivars had more chance of escaping the disease due to the lower temperatures in autumn. In addition, Hashiba (1985) found that the higher starch contents in the leaf blades and sheaths of late maturing cultivars inhibited the upward development of ShB.

A total of 106 entries in six *Oryza* species were inoculated with *R. solani* at IRRI. Disease incidence was recorded 15-20 days after flowering. All entries exhibited symptoms on the leaf sheath, but 35 entries were considered more tolerant than the susceptible control IR58. Accessions 101089 (*Oryza minuta*) and 100907 (*O. rufipogon*) were most resistant (Amante et al., 1991).

Development of novel resistance sources through mutation was tried by several researchers. Out of 48 γ -ray induced mutants of cultivar Nigersail, two were found to be partially resistant under field conditions in Bangladesh (Gangopadhyay and Padmanabhan, 1987). Mandal et al. (1995) developed 2500 somaclonal lines and tested them for ShB resistance. Of 27 highly resistant lines, five were from the cultivar Pokkali (highly susceptible to ShB) and 22 were from the cultivar BI16 (moderately resistant to ShB). Among 2100 R_2 somaclonal lines from U.S. long-grain cultivars screened for ShB resistance, three lines regenerated from the susceptible cultivar Labelle showed a high

level of resistance. In four years of greenhouse and field tests, the resistance was stable (Xie et al., 1990, 1992).

Genetic engineering may be a tool to generate novel high level ShB resistance in the near future. A 1.1 kilobase rice genomic DNA fragment containing a chitinase gene under the control of the CaMV 35S promotor was introduced into indica rice. Progeny from the chitinase-positive plants were tested for ShB resistance. The degree of resistance of the transgenic plants was found to be correlated with the level of chitinase expression (Lin et al., 1995).

1.5.3. MECHANISMS OF PARTIAL SHEATH BLIGHT RESISTANCE

Extensive physiological, biochemical, and histological studies on ShB indicated that there is no single common mechanism contributing to ShB resistance. Several early works showed that moderate levels of ShB resistance tends to be associated with tallness, less tillering, and late maturity characters (Kozaka, 1970; Ou, 1985). Manian (1984) tested 167 rice cultivars for ShB resistance and found that larger numbers of highly resistant and resistant cultivars were identified at early growth stages, such as tillering and booting. However, testing at the later growth stages identified more susceptible and highly susceptible cultivars. Resistant cultivars did exist in the milk or grain-filling stages. A similar relationship also has been reported by others working on the same or different diseases (Hashiba et al., 1977; Kahn and Libby, 1958; Marchetti and McClung, 1994). It was recommended that in screening trials, planting dates for cultivars from different maturity groups be adjusted so as to remove the masking effects caused by differences in the maturity of the plants.

Inhibitory effects of certain phenolic compounds on growth of and sclerotial production by the ShB fungus was reported by Kannaiyan and Prasad (1979). However, Zuber and Manibhushanrao (1984) failed to find the expected increase in total phenol content after inoculation with *R. solani* in both resistant and susceptible rice cultivars compared to preinoculation levels.

Hashiba et al. (1977) found that the starch content in leaf sheaths of early maturing cultivars ranged from 5.0-21.2 mg/g fresh weight. Mycelial growth on nitrogen-containing media amended with starch at the same range of concentrations was as good as that observed on these sheaths. On the contrary, starch content was higher in late maturing cultivars, ranging from 24.7-32.2 mg/g fresh weight. Fungal growth on media containing these levels of starch was reduced, suggesting that leaf sheaths of late maturing cultivars might be nutritionally less favorable for fungal growth than those of the early maturing cultivars.

Direct penetration of intact plant leaf tissues is often prohibited due to wax content (Marshall and Rush, 1980b; Massaquoi, 1986). Abundant waxes were observed on the outer sheaths of resistant cultivars, while few waxes were found on the outer sheaths of susceptible cultivars. Removal of waxes from resistant cultivars with chloroform followed by inoculation with *R. solani* resulted in a susceptible reaction (Marshall, 1979; Marshall and Rush, 1980b; Massaquoi, 1988). Two infection structures, infection cushion and lobate appressorium, are developed by ShB fungus during the infection of rice plants (Marshall, 1979). Highly significant correlations exist between disease severity ratings of the cultivars and both infection structure formation and culm

invasion. The fungus produces few infection structures on resistant cultivars, while producing more on susceptible cultivars (Marshall and Rush, 1980b).

1.5.4. INHERITANCE STUDIES

Hashioka (1951a and b) first conducted inheritance studies on ShB resistance. Eight cultivars showing moderate levels of partial resistance were studied. Of six F_2 populations from resistant x susceptible crosses, five showed a 3 resistant to 1 susceptible segregation ratio, which means a single dominant gene controlled the ShB resistance. Three of four resistant x resistant crosses showed no segregation. Because the classification of the F_2 individuals into infection classes was somewhat arbitrary due to the variability of symptoms of the segregates, it was not clear whether the inheritance of resistance was monogenic or bigenic.

Masajo (1976) studied the inheritance of partial ShB resistance from the moderately resistant cultivars Caloro and Zenith. Resistance to ShB was found to be partially dominant over susceptibility. The difference in ShB infection between the moderately resistant and very susceptible parents may have been due to as few as two pairs of genes. Broad sense heritability estimates ranged from 62.6-86.3%, while narrow sense heritability estimates only ranged from 3.6-20.1%. Results from a study of inheritance of the ShB resistance of the Rice/Grass (RG) dwarf rice line obtained by Dr. M. C. Rush (Department of Plant Pathology and Crop Physiology at Louisiana State University, Baton Rouge, LA) from China indicated that resistance was dominant over susceptibility. The high level of resistance in RG appeared to be controlled by three, independently inherited, dominant genes (Jeutong, 1985). Genetic studies suggested that

the partial ShB resistance in L201, RU7902185, and RU7902191 appeared to be controlled by two pairs of complementary genes, with resistance being dominant or partially dominant over susceptibility (Goita, 1985).

Genetic studies of moderate partial ShB resistance in T196, a line derived from Leah/RU8003050, was conducted by Marchetti and McClung (1994). Of 298 random F_3 lines from reciprocal Rosemont/T196 crosses, 24.8% rated as highly susceptible. The reciprocal cross means for ShB differed by ± 0.2 rating scale based on a 0-9 scale in both generations indicating no important maternal effects. The distribution of the F_3 lines was skewed towards the resistant side. Sheath blight ratings were found to be negatively correlated with days to heading ($r=0.63$).

Xie et al. (1990, 1992) screened 2100 R_2 somaclonal lines from U.S. long-grain cultivars for ShB resistance. Three lines regenerated from the susceptible cultivar Labelle showed a high level of resistance. In four years of greenhouse and field tests, the resistance was stable. The inheritance of sheath blight resistance in SC 86-20001-5 (LSBR-5) was controlled by a single recessive gene. Two independently inherited recessive genes controlled the partial ShB resistance in SC 86-20001-33 (LSBR-33).

However, many researchers attribute moderate or partial ShB resistance to such characters as late maturity and plant height. These researchers consider ShB resistance to be polygenically inherited (Hashiba et al., 1982; Li et al., 1995).

Sha and Zhu (1989, 1990) studied the inheritance of moderate levels of partial ShB resistance in six cultivars including Tetep, IET4699, and Jawa No. 14. The results indicated that the ShB resistance was a quantitative trait governed by at least three

genes. Heritability estimates (both broad sense and narrow sense) were low for all the resistant x susceptible crosses. Diallel analysis revealed that both additive and non-additive effects exerted significant influences on the inheritance of ShB resistance, however, the former appeared to be more important.

Using 255 bulked F_4 populations from a cross between the partially resistant cultivar Teqing and the susceptible cultivar Lemont, two years of field disease evaluation, and 113 well-distributed RFLP markers, Li et al. (1995) described six quantitative trait loci (QTLs) located on six of the 12 rice chromosomes that collectively explain approximately 60% of the genotype variation or 47% of the phenotypic variation. One of these resistance QTLs (*QSbr4a*), which accounted for 6% of the genotypic variation in resistance to *R. solani*, appeared to be independent of associated morphological traits. After studying the segregation of F_1 , F_2 , F_3 , F_4 , and BC_1 populations from the crosses between resistant cultivars Teqing and Jasmine 85 and susceptible cultivars Maybelle and Cypress, Pan et al. (1998) reported that two independently inherited dominant genes controlling the partial ShB resistance in those two resistant cultivars.

1.6. OBJECTIVES OF THIS STUDY

The objectives of this research were to: 1) evaluate and compare procedures used for genetic studies of ShB resistance on a set of cultivars and germplasms with different levels of partial ShB resistance under the same environmental conditions, 2) determine the mode-of-inheritance of ShB resistance in six cultivars or selected germplasms that have high levels of partial resistance, 3) compare the allelic relationships of major ShB

resistance genes among six test cultivars or lines, and with the ShB resistance of the registered elite line LSBR-5 (with one recessive gene).

CHAPTER 2. EVALUATION OF INOCULATION METHODS AND ASSESSMENT SYSTEMS FOR STUDYING INHERITANCE OF SHEATH BLIGHT RESISTANCE IN RICE

2.1. INTRODUCTION

Development of resistant rice cultivars could help control sheath blight (ShB). Because of the sporadic nature of epidemics, selection of resistant genotypes requires artificial inoculation. A number of systems of disease inoculation and assessment have been used to test disease reactions of different rice genotypes (Sharma et al., 1990a; Wasano et al., 1982; Ou, 1985). Yoshimura and Nishizawa (1954) first reported that straw culture of *Rhizoctonia solani* Kühn inserted among tillers of rice plants and evaluated after two months worked well in an irrigated field. The stem-tape-inoculation method developed by Amin (1975) was found to be effective in differentiating between resistant and susceptible genotypes under low humidity conditions. Sharma et al. (1990a) compared the effectiveness of four inocula, mycelia, rice grain/hull mixture, sclerotia, and naturally infected rice stems, for inducing ShB. The results indicated that infected rice stem inoculum produced the smallest area under the disease progress curve (AUDPC) compared to the other inoculum types. The three other inoculum sources were equally effective for inciting ShB development under screen house conditions. A syringe inoculation method was developed by Wasano et al. (1982). A 0.25 ml aliquot of crushed *R. solani* mycelia was injected into the third leaf sheath interstice at the heading stage. This method was found to be the most efficient and reliable compared with three other methods: pieces of rice straw, rice grain/hull mixture, and fungal disks.

All rice plant foliage, including the leaf blade, leaf sheath, and panicle, can be infected by *R. solani*. A precise, reliable assessment method is important for the discrimination of individual genotypes among a segregating rice population. After comparing five assessment methods, highest relative lesion height (HRLH; %), disease severity (DS; %), disease incidence (DI; %), standard evaluation system (SES; 0-9 scale), and real area infected (RAI; %), on three rice cultivars at IRRI, Sharma et al. (1990c) reported that HRLH and DS are the most convenient and dependable assessment methods. They are easy to use and accurately discriminate among cultivars. The DI and SES methods are not recommended because they do not give an accurate assessment or a quantitative measure of real infection, respectively. A reduced number of infection cushions produced by *R. solani* and a dark zone around smaller lesions also were suggested as effective methods to select for ShB resistance (Groth and Nowick, 1992; Dath, 1985).

For genetic studies on ShB resistance, an effective inoculation method should be able to create a reproducible and adequate amount of disease on each individual rice plant from a segregating population, while minimizing the number of escapes. A reliable assessment system should be able to discriminate sharply among segregating progenies. However, most current inoculation methods and assessment systems were developed to test populations of homozygous genotypes (Amin, 1975; Yoshimura and Nishizawa, 1954; Sharma et al., 1990a and c).

Different inoculation methods and assessment systems used by different researchers may contribute to the controversies concerning the mode of inheritance of

partial ShB resistance (Sha et al., 1990; Masajo, 1976; Guo et al., 1985). Most inheritance studies on partial ShB resistance carried out in the U.S. were done in the greenhouse at the seedling stage using rice hull/grain inoculum (Hoff et al., 1984 and 1985). The disease reaction was measured in various ways, including a 0-5 rating scale (Masajo, 1976), a 0-9 rating scale (Goita, 1985), disease severity based on the percentage of tissue infected (Masajo, 1976), and relative lesion height (Jeutong, 1985). However, in reports from other countries, the ShB reaction of segregating progenies was tested in the field using rice straw inoculum at later growth stages (Hashioka, 1951; Sha et al. 1990). No comparison of multiple inoculation methods and assessment systems under uniform conditions has been reported.

Accurate evaluation of existing rice genotypes and new breeding lines for resistance to ShB requires the implementation of uniform, reliable inoculation and assessment systems. The purpose of this study was to compare four field inoculation methods and five assessment systems for their ability to differentiate among rice genotypes with known levels of ShB resistance.

2.2. MATERIALS AND METHODS

2.2.1. PLANT MATERIALS

Nine rice genotypes were evaluated (Table 1). These materials were chosen to represent a range of levels of ShB resistance. The agronomic characteristics of these genotypes are provided in Table 1.

Table 1. Geographic origin, agronomic characters, and sheath blight reactions of rice genotypes used to evaluate inoculation methods and disease assessment systems.

Genotype	Origin	Grain type	Days to 50% heading	Plant height ^a (cm)	Sheath blight reaction ^b
Cypress	U.S.A.	Long	76	74	HS
Maybelle	U.S.A.	Long	71	77	HS
Bengal	U.S.A.	Medium	77	74	S
Rice/Grass	China	Medium	87	81	MS
Gui Chao	China	Medium	83	84	MR
Teqing	China	Medium	86	96	MR
Jasmine 85	U.S.A./IRRI	Long	87	83	MR
LB86-30344	U.S.A./LSU	Long	96	112	R
H ₄ /CODF	Sri Lanka	Long	91	100	R

^a Height measured from root to collar of flag leaf.

^b HS = Highly susceptible; S = susceptible; MS = moderately susceptible; MR = moderately resistant; R = resistant.

2.2.2. FIELD EXPERIMENTS

Two experiments were conducted at the LSU Rice Research Station in Crowley, LA from 1995 to 1997. The first experiment was designed to test four inoculation methods, and the second experiment was designed to test five assessment systems.

For the inoculation method experiment, the experimental design was a split-plot with genotype as the main-plot factor and inoculation method as the subplot factor. The main-plot factor was replicated three times in both 1995 and 1996. Each main plot consisted of eight, 2.4 m long rows with a 25.4 cm spacing between rows. Each subplot consisted of one inoculated row separated by a noninoculated row. This experiment was planted on May 18, 1995 and April 11, 1996.

For the assessment system evaluation, a complete randomized block design was applied with genotype as the treatment and two blocks. Each plot consisted of eight, 2.4 m rows with a 25.4 cm spacing between rows. This experiment was planted on April 23,

1997. After the permanent flood was applied, plants were thinned or adjusted to 20-25 plants per row.

2.2.3. INOCULUM PREPARATION

LR172, a highly aggressive isolate of *R. solani* originally isolated from infected “Bluebonnet” rice by M. C. Rush of the Department of Plant Pathology and Crop Physiology, Louisiana State University was used in these experiments (Masajo, 1976). Sclerotia formed on potato dextrose agar (PDA) medium were kept at 4°C and subcultured every 2 months. The four inocula evaluated in the first experiment were prepared based on the following procedures: (1) MIX - one part rice grain was mixed with to two parts rice hulls by volume and then placed in 2-liter flasks. Water was added to the flasks in a ratio of one part water to two parts mixture on a volume basis. The flasks were autoclaved on two consecutive days at 121°C for 30 minutes each time. Plugs from a 5-day old culture of *R. solani* growing on PDA were transferred into the sterilized flasks. Inoculated flasks were cultured at room temperature for 21 days. (2) STRW - healthy, strong rice culms were selected and cut into 15-18 cm long pieces. Before autoclaving at 121°C for 30 minutes, the straw pieces were submerged in 2% sucrose solution for 30 minutes, then put into 2-liter flasks. Sterilized rice straw pieces were inoculated with plugs of *R. solani* and cultured at room temperature for 21 days. (3) TP - toothpick tips 0.5 cm long were washed in tap water and put into a glass petri dish. Potato dextrose broth (PDB) medium was added to the petri dish in a ratio of one part PDB to one part toothpick tips on a volume basis. The petri dish was autoclaved at 121°C for 30 minutes, allowed to cool, and inoculated with plugs of *R. solani*.

Inoculated toothpick tips were cultured at room temperature for 10 days. (4) BR - brown rice was washed and submerged in tap water for 12 hours. After autoclaving at 121°C for 30 minutes, the brown rice was inoculated with plugs of *R. solani* and cultured at room temperature for 21 days.

2.2.4. INOCULATION METHODS AND ASSESSMENT SYSTEMS

For the inoculation method experiment, the four test inocula were applied as follows: (1) MIX - a rectangular frame measuring 2.4 m x 0.25 m made from polyethylene sheeting and wood stakes was used to isolate each subplot before inoculation. About 50 ml inoculum was evenly distributed among each subplot of one row by hand. (2) STRW - one or two pieces of rice straw culture were inserted into each rice hill, then all tillers in the hill were tightened with a string to facilitate disease development. (3) TP - one toothpick tip inoculum was inserted into a fully extended sheath just behind the ligule. (4) BR - a cultured grain was inserted into a fully extended sheath just behind the ligule. For MIX and STRW, inoculation was done 67-68 days after planting (at the maximum tillering stage), while for TP and BR, inoculation was done 75-84 days after planting (at the booting stage). Disease incidence (INCI) and severity (RAT9) were recorded 20 days after inoculation and 30 days after heading, respectively. The means of each subplot were used for statistical analysis.

Five assessment systems tested in the second experiment were: (1) RAT9 - the 0-9 rating scale described by Rush et al. (1976), where 0 = no symptoms; 1 = oval lesions restricted at water line or inoculation points, broad red-brown or purple-brown border, less than 2.5% tissues affected; 2 = few oval or coalesced lesions on lower sheaths or at

infection points, 5% or less of tissues affected; 3 = lesions on lower leaf sheaths, less than 10% of tissues affected; 4 = lesions mainly restricted to sheaths on lower third of plant, 10-15% of leaf blade and sheath tissues affected; 5 = lesions mainly restricted to lower half of plants, 15-25% of tissues affected, culm not injured; 6 = lesions usually coalescing and affecting lower 2/3 of sheath area of plant, 25-40% of tissues affected, culm usually not affected; 7 = lesions usually coalescing and affecting lower 3/4 of sheath area of plant, lesions extending to leaf blades of lower 2/3 of plant, 40-60% of tissues affected, outer portion of culm may be brown; 8 = lesions reaching to flag leaf, lower sheaths with coalesced lesions covering most of tissues, lower and middle leaves dead or dying, 60-90% of tissues affected, culms with brown streaks; 9 = lesions reaching to flag leaf, lower leaves mostly dead, sheaths dried, culms brown, water-soaked or collapsing, most of tillers lodged. (2) INCI - the percentage of infected tillers out of a 25-tiller sample. (3) LH - uppermost lesion height in cm measured from the crown to the collar of the uppermost leaf. (4) RLH - ratio of uppermost lesion height on sheath divided by plant height (from root to the junction of leaf blade and sheath of the uppermost extended leaf). (5) DS - visually estimated percentage of diseased area of both leaf and sheath.

For the assessment system evaluation, all plots were inoculated by the MIX method 76 days after planting (at the maximum tillering stage or booting stage). Disease development was assessed by RAT9, INCI, LH, RLH, and DS. Data based on the first four systems were recorded every week for 7 weeks, however, DS was only measured

once, 30 days after heading. Plot means were used for statistical analysis. AUDPCs for the first four systems were calculated by the following formula (Sharma et al., 1990a):

$$\text{AUDPC} = \sum \frac{X_i + X_j}{2} \times 7$$

where X_i = disease score of last measurement

X_j = disease score of present measurement

\sum = summation up to seven weeks.

2.2.5. STATISTICAL ANALYSIS

Analysis of variance was performed by using SAS PROC GLM (SAS, 1988). Data for INCI and RLH were transformed by arcsin (x), and data for RAT9 by square root (x+1) before analysis of variance. The main effects of genotype and inoculation method, and their interactions were evaluated. Means separation was determined by Duncan's multiple range test. The relationships among different inoculation methods and different assessment systems were obtained by Spearman's rank correlation using SAS CORR procedures.

2.3. RESULTS

2.3.1. COMPARISON OF DIFFERENT INOCULATION METHODS

Significant year by genotype and year by inoculation method interactions for both incidence and severity were detected in the initial analysis. Therefore, data from experiment one were analyzed separately for each year.

A highly significant difference ($P < 0.01$) in disease incidence was found among rice genotypes and inoculation methods in both 1995 and 1996 (Table 2). No significant

genotype by inoculation method interactions were observed in either year. This indicated that the effects of inoculation methods on disease incidence were similar for different rice genotypes. The STRW method gave the highest disease incidence, while MIX method had the lowest one (Table 3). Disease incidence from BR, MIX, and TP methods was higher in 1996 than in 1995. This was probably due to difference in weather conditions between the two years. Although the total rainfall was 2002.3 mm in 1995 compared to 1404.6 mm in 1996, the number of rainy days from inoculation to disease assessment was 32 in 1996 compared to 13 in 1995. Apparently the high relative humidity contributed to the heavier disease in 1996. However, the STRW method gave consistent infection in both years, probably because tightening of rice plants allowed close contact of inoculum with rice tissues and maintained higher humidity inside the rice hill. All these factors make this method less affected by weather conditions. Maybelle, Cypress, Bengal, and Gui Chao consistently had the highest disease incidence, while H₄/CODF, and LB86-30344 had the lowest disease incidence. This indicated that H₄/CODF and LB86-30344 may possess resistance mechanisms that inhibit initial infection by *R. solani*. The high disease incidence of moderately resistant genotypes such as Jasmine 85, Teqing, and Gui Chao also verified the partial resistance nature of this disease.

Disease severity varied significantly ($P<0.01$) among rice genotypes and inoculation methods in 1995 and 1996 (Table 2). A genotype by inoculation method interaction detected in both years was highly significant ($P<0.01$) in 1996, while significant ($P<0.05$) in 1995. In both years, H₄/CODF and LB86-30344 consistently had the lowest disease ratings when tested by different inoculation methods. In contrast,

Maybelle, Cypress, and Bengal had the highest disease ratings (Table 4). Variation was observed for disease reactions of moderately resistant genotypes under different inoculation methods and over years. The STRW method induced the highest disease ratings, while the TP method was associated with the lowest ones. Compared with the STRW method, MIX has more power to differentiate among genotypes. In 1996, the ShB reactions of nine tested genotypes could be separated into five distinct groups with the MIX method, however, only four groups could be distinguished with the STRW method. The MIX method separated Jasmine 85 from Gui Chao, but the STRW method failed to do so. The similar reactions of the tested genotypes to the two methods may be due to the low disease pressure.

Spearman's rank correlation coefficients among the four inoculation methods are shown in Table 5. For disease incidence, significant or highly significant positive correlations were observed between STRW and MIX, and between BR and TP methods in both 1995 and 1996. Significant positive correlations between BR and STRW and between TP and MIX were only found in 1996. This may be due to the similarities between the BR and TP methods and between the STRW and MIX methods. In the BR and TP methods, inoculation was done on each individual tiller, while in STRW and MIX, inoculation was done on each row or whole plant. For disease severity, significant or highly significant positive correlations were found between each pair of inoculation methods. When disease pressure was high, as in 1996, all four methods gave almost the same ranking of tested rice genotypes (Tables 4 and 6).

Table 2. Sources of variation, degrees of freedom (df) and mean square values for disease incidence (INCI) and severity (RAT9) for analysis of four inoculation methods used to determine sheath blight resistance of nine rice genotypes in field experiments conducted in 1995 and 1996 at the Rice Research Station, Crowley, LA.

Year	Source	df	INCI	RAT9
1995				
	Block	2	0.0010	0.1056***
	Genotype	8	0.1872**	1.7351**
	Block*genotype	16	0.0088	0.0373
	Method	3	0.8470**	1.7454**
	Genotype*method	24	0.0247	0.0390*
	Error	54	0.0159	0.0210
1996				
	Block	2	0.0049	0.0133*
	Genotype	8	0.1934**	2.4653**
	Block*genotype	16	0.0147	0.0064
	Method	3	0.2666**	1.0351**
	Genotype*method	24	0.0239	0.0383**
	Error	54	0.0177	0.0084

* *, ** = Significant at the 0.05 and 0.01 level, respectively.

Table 3. Mean disease incidence (percentage of tillers infected) and rankings (in parentheses) of nine rice genotypes inoculated with *Rhizoctonia solani* using four inoculation methods (BR = brown rice, MIX = rice grain/hull mixture, STRW = rice straw, TP = toothpick tip) in field tests at the Rice Research Station, Crowley, LA in 1995 and 1996.

Year	Genotype	BR	MIX	STRW	TP
1995	Bengal	73.3 ab ^x (4) ^y	83.7 bc (6)	98.3 a (5)	80.0 bc (4)
	Cypress	76.7 ab (5)	90.7 ab (8)	100.0 a (6)	86.7 ab (6)
	Gui Chao	76.7 ab (5)	85.3 bc (7)	98.3 a (5)	83.3 b (5)
	H ₄ /CODF	66.7 b (2)	73.3 cd (3)	92.0 a (2)	76.7 bc (3)
	Jasmine 85	76.7 ab (5)	78.7 bc (4)	95.3 a (3)	73.3 bc (2)
	LB86-30344	60.0 c (1)	56.7 e (1)	90.7 a (1)	70.0 c (1)
	Maybelle	86.7 a (7)	100.0 a (9)	100.0 a (6)	96.7 a (7)
	Rice/Grass	83.3 a (6)	65.3 de (2)	96.7 a (4)	86.7 ab (6)
	Teqing	70.0 bc (3)	81.3 bc (5)	100.0 a (6)	73.3 bc (2)
1996	Bengal	96.7 ab (3)	93.0 ab (6)	100.0 a (5)	96.7 a (3)
	Cypress	96.7 ab (3)	98.7 a (8)	100.0 a (5)	96.7 a (3)
	Gui Chao	96.7 ab (3)	93.3 ab (7)	99.7 a (4)	93.3 a (2)
	H ₄ /CODF	76.7 c (1)	80.0 c (2)	95.3 ab (2)	83.3 b (1)
	Jasmine 85	100.0 a (4)	92.7 ab (5)	100.0 a (5)	100.0 a (4)
	LB86-30344	90.0 b (2)	65.0 d (1)	89.7 b (1)	93.3 a (2)
	Maybelle	96.7 ab (3)	100.0 a (9)	100.0 a (5)	100.0 a (4)
	Rice/Grass	96.7 ab (3)	81.3 c (3)	98.3 a (3)	93.3 a (2)
	Teqing	96.7 ab (3)	86.0 bc (4)	100.0 a (5)	93.3 a (2)

^x Means within columns and year followed by the same letter are not significantly different at the 0.05 level, according to Duncan's multiple range test.

^y Rank of disease reaction among tested rice genotypes.

Table 4. Mean disease severity (0-9 rating)* and rankings (in parentheses) of nine rice genotypes inoculated with *Rhizoctonia solani* using four inoculation methods (BR = brown rice, MIX = rice grain/hull mixture, STRW = rice straw, TP = toothpick tip) in field tests at the Rice Research Station, Crowley, LA in 1995 and 1996.

Year	Genotype	BR	MIX	STRW	TP
1995					
	Bengal	4.9 b ^x (7) ^y	7.6 a (7)	7.9 a (7)	4.7 b (6)
	Cypress	5.8 b (8)	8.5 a (8)	8.8 a (9)	5.4 b (7)
	Gui Chao	3.1 c (4)	4.1 c (4)	5.5 c (3)	3.2 c (5)
	H ₄ /CODF	2.0 d (1)	2.7 d (2)	3.4 d (1)	1.8 d (1)
	Jasmine 85	3.0 cd (3)	4.0 c (3)	5.7 c (4)	3.2 c (5)
	LB86-30344	2.6 cd (2)	2.4 d (1)	3.9 d (2)	2.6 cd (3)
	Maybelle	7.4 a (9)	8.6 a (9)	8.6 a (8)	6.7 a (8)
	Rice/Grass	3.2 c (5)	5.5 b (6)	6.8 b (6)	3.1 c (4)
	Teqing	3.5 c (6)	4.5 bc (5)	5.9 bc (5)	2.4 cd (2)
1996					
	Bengal	5.6 b (7)	5.9 b (7)	7.8 b (7)	5.8 b (6)
	Cypress	8.0 a (8)	8.2 a (8)	8.8 a (8)	8.2 a (7)
	Gui Chao	3.5 cd (5)	4.5 c (5)	5.7 c (4)	3.0 c (4)
	H ₄ /CODF	2.1 e (1)	2.4 e (2)	3.4 d (2)	2.1 d (2)
	Jasmine 85	3.1 d (3)	3.8 d (3)	5.5 c (3)	2.9 c (3)
	LB86-30344	2.2 e (2)	2.2 e (1)	3.3 d (1)	2.0 d (1)
	Maybelle	8.3 a (9)	8.3 a (9)	9.0 a (9)	8.3 a (8)
	Rice/Grass	3.9 c (6)	5.6 b (6)	7.4 b (6)	3.4 c (5)
	Teqing	3.2 d (4)	4.3 cd (4)	6.0 c (5)	3.0 c (4)

* Based on a 0-9 rating scale where 0 = no symptoms and 9 = plants dead at maturity (Rush et al., 1976).

^x Means within columns and year followed by the same letter are not significantly different at the 0.05 level, according to Duncan's multiple range test.

^y Rank of disease reaction among tested rice genotypes.

Table 5. Spearman's rank correlations of disease incidence (percent of tillers infected) for four inoculation methods (BR = brown rice, MIX = rice grain/hull mixture, STRW = rice straw, TP = toothpick tip) tested on nine rice genotypes in field tests at the Rice Research Station, Crowley, LA in 1995 and 1996.

Year	Method	BR	MIX	STRW
1995				
	MIX	0.62		
	STRW	0.62	0.89***	
	TP	0.83**	0.65	0.51
1996				
	MIX	0.66		
	STRW	0.76*	0.89**	
	TP	0.76*	0.76*	0.59

* , ** = Significant at the 0.05 and 0.01 level, respectively.

Table 6. Spearman's rank correlations of disease severity rating (0-9 rating)^a of four inoculation methods (BR = brown rice, MIX = rice grain/hull mixture, STRW = rice straw, TP = toothpick tip) tested on nine rice genotypes in field tests at the Rice Research Station, Crowley, LA in 1995 and 1996.

Year	Method	BR	MIX	STRW
1995				
	MIX	0.97*** ^b		
	STRW	0.95**	0.95**	
	TP	0.77*	0.77*	0.79*
1996				
	MIX	0.98**		
	STRW	0.97**	0.98**	
	TP	0.97**	0.99**	0.99**

^a Based on a 0-9 rating scale where 0 = no symptoms and 9 = plants dead at maturity (Rush et al., 1976).

^b * , ** = Significant at the 0.05 and 0.01 level, respectively.

2.3.2 COMPARISON OF ASSESSMENT SYSTEMS

Table 7 shows the analysis of variance of ShB ratings from five assessment systems on six rice genotypes inoculated with MIX inoculum. No significant differences in ShB resistance were detected from INCI data. This indicates that disease incidence is

probably not a good measure for ShB resistance, especially in artificially inoculated trials. Highly significant differences in ShB resistance were detected by the other four assessment systems. Lemont had the highest AUDPCs or DS, while H₄/CODF and LB86-30344 consistently had the lowest AUDPCs or DS (Table 8). This implies that these two genotypes may possess the mechanisms to retard disease development after infection occurs in addition to inhibiting initial infection. Jasmine 85 had the second highest INCI and LHT values, but had a small DS and low RAT9. Apparently, both INCI and LHT lack the ability to differentiate rice genotypes with a moderate level of ShB resistance. Compared with RLH and DS, the RAT9 has more power to differentiate among rice genotypes with different levels of ShB resistance.

Spearman's rank correlation coefficients among the five assessment systems are shown in Table 9. Highly significant positive correlations were observed between each pair of three assessment systems, RAT9, RLH, and DS. Disease incidence (INCI) was only significantly correlated with the direct (LHT) or indirect (RLH) lesion height readings. The lesion height readings were significantly correlated.

Table 7. Sources of variation, degrees of freedom (df) and mean square values for five assessment systems (INCI = disease incidence, RAT9 = disease severity rating, RLH = relative lesion height, LHT = lesion height, and DS = disease severity) used to determine sheath blight resistance of six rice genotypes inoculated *Rhizoctonia solani* in a field experiment at the Rice Research Station, Crowley, LA in 1997.

Source	df	INCI	RAT9	RLH	LHT	DS
Block	1	2.36	36.7500	16206.75	1474.08	72.52
Genotype	5	117.21	15934.604***	530393.15**	145605.95**	1370.22**
Error	5	33.36	444.822	16853.55	12371.68	79.92

* *, ** = Significant at the 0.01 level.

Table 8. Area under the disease progress curve (AUDPC) or mean scores, and rankings (in parentheses) of five assessment systems (INCI = disease incidence, RAT9 = disease severity rating, RLH = relative lesion height, LHT = lesion height, and DS = disease severity) applied to six rice genotypes inoculated with *Rhizoctonia solani* in a field test at the Rice Research Station, Crowley, LA in 1997.

Genotype	AUDPC					DS
	INCI	RAT9	RLH	LHT		
Bengal	3892 abc ^x (4) ^y	169.40 b (5)	1718.5 b (5)	1144.5 bc (3)		39.50 b (5)
H ₄ /CODF	3136 bc (2)	69.65 d (1)	962.5 c (1)	808.5 d (1)		4.75 c (1)
Jasmine 85	4606 ab (5)	127.75 bc (3)	1522.5 b (4)	1326.5 ab (5)		18.00 bc (3)
LB86-30344	2968 c (1)	80.85 cd (2)	1053.5 c (2)	997.5 cd (2)		6.50 c (2)
Lemont	4830 a (6)	316.40 a (6)	2390.5 a (6)	1592.5 a (6)		74.00 a (6)
Teqing	3514 abc (3)	143.15 b (4)	1498.0 b (3)	1176.0 bc (4)		19.00 bc (4)

^x Means within columns followed by the same letter are not significantly different at the 0.05 level, according to Duncan's multiple range test.

^y Rank of disease reaction among tested rice genotypes.

Table 9. Spearman's rank correlations of area under the disease progress curve (AUDPC) or mean scores of five assessment systems (INCI = disease incidence, RAT9 = disease severity rating, RLH = relative lesion height, LHT = lesion height, and DS = disease severity) tested on six rice genotypes inoculated with *Rhizoctonia solani* in a field test at the Rice Research Station, Crowley, LA in 1997.

Assessment method	INCI	RAT9	RLH	LHT
RAT9	0.77			
RLH %	0.89 ^a	0.94 ^{**}		
LHT	0.89 [*]	0.77	0.83 [*]	
DS %	0.77	1.00 ^{**}	0.94 ^{**}	0.77

^a *, ** = Significant at the 0.05 and 0.01 levels, respectively.

2.4. DISCUSSION

Although extensive screening for complete resistance or immunity to ShB has been carried out, to date, only partial or incomplete ShB resistance is available (Rao, 1995; Dath, 1990; Ou, 1985). This resistance may be associated with morphological or physiological characters such as lateness, tallness of rice plants, or thick cuticle layer, and also may be expressed as fewer and smaller lesions surrounded by a dark brownish zone

(Groth and Nowick, 1992). To identify genotypes with partial ShB resistance from a segregating population, an ideal inoculation method which can provide equal opportunity for infection of each individual plant exposed to the inoculum under natural conditions, and an assessment system which will evaluate all symptoms in single infected plant or tiller must be employed. In this experiment, four inoculation methods along with five assessment systems were evaluated under field conditions from 1995 to 1997.

All four inoculation methods can cause more than 96% tiller infection for susceptible cultivars Cypress and Maybelle under conditions favorable for ShB development, such as in 1996. However, they vary in their ability to cause infection in resistant rice genotypes. Little difference in disease incidence was found between resistant and susceptible rice genotypes tested with the STRW method, however highly significant differences in disease severity measured by RAT9 were observed in both 1995 and 1996. When tested by the MIX method, H₄/CODF, LB86-30344, and Rice/Grass had much lower disease incidence than the other genotypes. This suggested that these genotypes may possess a mechanism to inhibit the initial infection by *R. solani* in addition to mechanisms which may retard the postinfectious development of the pathogen. This preinfection defense mechanism can not be detected by the STRW method. The higher disease incidences of Gui Chao and Jasmine 85 suggest that both of them lack such a mechanism. When tested by the STRW method, only H₄/CODF and LB86-30344 showed a resistant reaction, while moderately resistant genotypes Gui Chao, Teqing, and Jasmine 85 showed susceptible reactions. The large amount of initial inoculum or unnatural microclimatic conditions created by tightening the inoculated rice

plant with a string may contribute to the failure of this method to differentiate among the genotypes. Disease was less severe when induced by the BR and TP methods. Based on the 0-9 rating scale, the BR and TP methods were unable to distinguish the moderately resistant genotypes Jasmine 85, Teqing, and Gui Chao from a moderately susceptible one such as Rice/Grass. Inoculation with these two methods was time consuming, limiting their application to small populations or greenhouse experiments. In contrast, the MIX method was easy to apply. With limited labor, large populations can be tested simultaneously. Better separation of resistant and susceptible rice genotypes also was obtained with the MIX method, and it may be the most efficient for identifying true differences in ShB resistance.

Among the five assessment systems, INCI did not differentiate between resistant and susceptible genotypes. LHT failed to separate moderately resistant Jasmine 85 from highly susceptible Lemont. However, RAT9, RLH, and DS showed similar effectiveness in separating resistant and susceptible genotypes. After testing on three rice cultivars, Sharma et al. (1990c) also concluded that RLH and DS were the most convenient and dependable assessment methods because they are easy to use and discriminate among cultivars.

CHAPTER 3. INHERITANCE OF PARTIAL SHEATH BLIGHT RESISTANCE IN SIX RICE GENOTYPES

3.1. INTRODUCTION

Sheath blight (ShB), caused by *Rhizoctonia solani* Kühn, is one of the most important rice diseases in the world. Severe infection of commercial rice cultivars by this disease may result in poor grain filling, lodging, low grain quality, and poor yield. It is difficult to control ShB disease with cultural practices (Lee and Rush, 1983). Chemical control is effective, but it is expensive and may cause environmental concern (Groth and Rush, 1988; Groth et al., 1996). Therefore, breeding and utilization of resistant cultivars is the only practical and economic way to control this disease.

To date, no complete ShB resistance has been identified, only moderate or partial resistance is available (Lee and Rush, 1983). Partial resistance can offer adequate protection against the pathogen under field conditions (Rao, 1995; Li et al., 1995). Several genetic studies have been conducted using partially resistant cultivars. The results have been fragmentary and controversial. In 1951, Hashioka reported that partial ShB resistance in five cultivars was controlled by one or two dominant genes. Later, several reports suggested that partial ShB resistance from several germplasms when crossed to susceptible U. S. long-grain cultivars was conferred by one or two completely or partially dominant genes (Masajo, 1976; Goita, 1985; Hoff et al., 1984; Hoff et al. 1985). Recently, two elite ShB resistant lines were developed through somaculture of the susceptible U.S. cultivar Labelle and development of somaclonal variation (Xie et al., 1990; Xie et al., 1992). The resistance in these lines was conferred by one or two

recessive genes. Some positive progress has been made in breeding resistant cultivars using those somaclonal variants (Rush et al., 1995; Rush et al., 1996).

Some researchers attribute partial sheath blight resistance to such characters as late maturity, plant tallness, and low tiller number, and they consider the resistance to be quantitatively inherited (Hashiba et al., 1982; Li et al., 1995). After analyzing the resistance of several indica cultivars, including Tetep, IET4699, Retna, and Kataktara Da2, Zhu and Sha (1990) reported that the resistance of these cultivars was polygenically inherited. Li et al. (1995) reported that six quantitative trait loci (QTLs) for partial sheath blight resistance in Teqing were located on six of the 12 rice chromosomes and collectively explained approximately 60% of the genotype variation or 47% of the phenotypic variation. One of these resistance QTLs (*QShb4a*), which accounted for 6% of the genotypic variation in resistance to *R. solani*, appeared to be independent of associated morphological traits. After studying the segregation of F₁, F₂, F₃, F₄, and BC₁ populations from crosses between the resistant cultivars Teqing and Jasmine 85 and the susceptible cultivars Maybelle and Cypress, Pan et al. (1998) reported that two independently inherited dominant genes controlled the partial ShB resistance in those two resistant cultivars.

However, these fragmentary results do not satisfactorily explain the inheritance of ShB resistance in rice. The objective of this research was to study the mode-of-inheritance of partial resistance to rice ShB in six genotypes crossed with the susceptible cultivar Lemont by developing segregating F₂ populations and F₃, F₄, and BC₁

populations to provide genetic information for rice breeding programs for using partial ShB resistance.

3.2. MATERIALS AND METHODS

3.2.1. PLANT MATERIALS

Six rice genotypes with proven partial ShB resistance were studied in this experiment. They included: H_4 /CODF, a mutant derived from the Sri Lanka cultivar H_4 by cobalt irradiation; LB86-30344, a somaclonal line derived from the ShB susceptible U.S. long-grain cultivar Labelle; Jasmine 85, an aromatic cultivar selected from an International Rice Research Institute (IRRI) line and released in the U.S.; and Teqing, Gui Chao, and Yangdao 4, indica type commercial cultivars released in China. Lemont, a U.S. long-grain cultivar highly susceptible to sheath blight, was used as the common susceptible parent in all crosses to provide a uniform genetic background for the partial ShB resistance in segregating populations.

Reciprocal crosses between resistant genotypes Jasmine 85, Gui Chao, LB86-30344, and Teqing and the susceptible cultivar Lemont were made in the summer of 1994, while Gui Chao and Yangdao 4 crosses with Lemont were made in the summer of 1995. The F_1 s of the Jasmine 85 x Lemont and (H_4 /CODF) x Lemont crosses were backcrossed to the respective resistant and susceptible parents. The hybrid seeds were first treated with 1% (v/v) Vitavax 200 for 5 minutes, then germinated on a sheet of wet cheesecloth which was supported by a metal hardware cloth frame that contacted a water reservoir inside a covered plastic container. After 1 week, the seedlings were transplanted to pots containing a soil mixture consisting of 2 parts steam-sterilized

Olivier silt loam soil, 1 part washed sand, and 1 part peat moss by volume. Plants were maintained in a greenhouse. Parent plants were planted along with the hybrids to facilitate the identification of possible selfed plants among the hybrids. At maturity, the seeds were bulk-harvested for each cross. In some cases, the cut rice stalks were fertilized with nitrogen and a ratoon crop was grown to produce more F_2 seeds. From the F_2 populations, seeds from about 150 individual plants were randomly harvested from each cross at maturity, and they were separately threshed and stored to be planted as F_3 lines the next year. For each of the crosses Jasmine 85 x Lemont, Teqing x Lemont, and LB86-30344 x Lemont, the seeds from each F_2 plant were divided into two parts. One part was stored in the refrigerator for 1 year and planted in the following season, and another part to be planted in the next year as F_3 to produce $F_{2,4}$ seeds. Ninety F_3 lines of each cross with more than seven plants were randomly bulk-harvested to be planted as $F_{2,4}$ lines.

3.2.2. FIELD EXPERIMENTS

All experiments were conducted in field plots at the Louisiana State University Rice Research Station in Crowley, LA from 1995 to 1997. Plants were grown in tiers of 2.4 m rows with a 25.4 cm spacing between rows. Plots of parents, F_2 , F_3 , and $F_{2,4}$ generations were planted with a Hege 90 Series Drill Planter using 12-cell magazines. Each cell contains about 50-60 seeds. Greenhouse grown seedlings of F_1 hybrids and BC_1 s were transplanted into the field after the permanent flood was applied. Normal cultural practices were followed with plots receiving 16-47-47 ($N-P_2O_5-K_2O$) kg/ha fertilizer drilled preplant and additional 50 kg/ha N top-dressed at the green ring stage.

Plots were treated with propanil and bensulfuron methyl herbicides and carbofuran insecticide for rice water weevil control. After the permanent flood was applied, directly seeded plants were thinned or adjusted to 20-25 plants per row. For each F_2 population, the parents and both reciprocal F_1 populations were tested in a completely randomized design with single row plots and three replicates. Depending on seed availability for each generation in each year, the number of parental, F_1 , and F_3 plants of each F_3 line evaluated was between 20 and 60, the number of F_2 plants was between 240 and 700, and the number of BC_1 plants was between 30 and 70. Because of the limited number of seeds for each F_3 line, only 50 F_3 and corresponding $F_{2.4}$ lines for Jasmine 85 x Lemont, 16 F_3 and corresponding $F_{2.4}$ lines for Teqing x Lemont, and 64 F_3 and corresponding $F_{2.4}$ lines for LB86-30344 x Lemont were included for a stability study in 1997. The test was conducted using a complete randomized block design with two blocks. A single, 2.1 m row consisting of 20-25 plants was considered a plot for each F_3 line, while two 2.1 m rows was considered a plot for each $F_{2.4}$ line. Both the F_3 line and its corresponding $F_{2.4}$ line were planted together to minimize the environmental effects.

3.2.3. INOCULATION AND DISEASE RATING

LR172, a highly-virulent *R. solani* isolate cultured on autoclaved 1:2 rice grain:rice hull mixture (Figure 1) was used as inoculum in this test (Rush et al., 1973). Plants were inoculated at the maximum tillering stage with 50 ml of inoculum scattered over each 2.4 m row (Figure 2). Disease ratings were made on individual plants based on a 0-9 rating scale where 0 = no disease and 9 = plant dead and collapsed at maturity 30-35 days after heading (Rush et al., 1976). For each segregating F_2 or BC_1 population, the



Figure 1. Inoculum of *Rhizoctonia solani*, highly-virulent isolate LR172, cultured on autoclaved 1:2 rice grain:rice hull mixture.



Figure 2. Inoculation of rice plants at the maximum tillering stage with 50 ml of *Rhizoctonia solani* rice grain/hull inoculum scattered over each 2.4 m row (Crowley, LA).

boundary between resistant and susceptible plants was determined by the pattern of the distribution of that population and the disease reactions of both parents. Individual plants of the F_3 and $F_{2:4}$ lines also were scored, and each line was classified as homozygous resistant, segregating, or homozygous susceptible.

3.2.4. STATISTICAL ANALYSIS

For the inheritance study, the goodness of fit of segregation ratios for all data was analyzed by the chi-square test. Duncan's multiple range test was applied to test the differences among both parents and reciprocal F_1 populations (SAS, 1988). Both F_3 and $F_{2:4}$ data were analyzed following the model for a completely randomized block design. Plot means were used for statistical analysis. Heritability, the ratio of genotypic variability to phenotypic variability, was calculated from the estimates of the parameters derived from the analysis of variance as follows:

Analysis of variance

Source of variation	df	Mean square	Expected mean square
Block	$r-1$		
Lines	$k-1$	MS1	$\sigma_e^2 + r \sigma_g^2$
Error	$(r-1)(k-1)$	MS2	σ_e^2

where:

k = number of F_3 or $F_{2:4}$ lines

r = number of blocks

σ_e^2 = variation of experimental error

σ_g^2 = variation of F_3 or $F_{2:4}$ lines.

Broad-sense heritability was estimated based on the following formula (Mather and Jinks, 1982; Foolad and Jones, 1992):

$$H^2 = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_e^2} \times 100\%$$

where: $\sigma_e^2 = \sigma_e^2/r$ = variation of experimental error for the mean of F_3 or $F_{2,4}$ lines.

The stability of sheath blight resistance was estimated by Pearson's correlation analysis using F_2 , F_3 , and $F_{2,4}$ data (SAS, 1988).

3.3. RESULTS

3.3.1. INHERITANCE OF PARTIAL SHEATH BLIGHT RESISTANCE FROM H_4 /CODF

Table 10 shows that the susceptible parent Lemont had a disease range from 6 to 9 with a mean rating of 8.0, while the resistant parent H_4 /CODF had a disease range from 1 to 4 with a mean rating of 3.0. Both reciprocal F_1 populations had mean disease ratings of 2.5 which was close to that of the resistant parent. No significant difference in mean disease rating was found between the reciprocal F_1 populations. This indicated that the partial sheath blight resistance in H_4 /CODF was a dominant character, and maternal effects were not important. The narrow range of disease rating for both reciprocal F_1 populations may be due to the transplanting of the seedlings which made F_1 plants evenly spaced and, therefore, equally exposed to the fungal pathogen.

Table 10. Sheath blight reaction of parents and the F_1 generations from reciprocal crosses between the susceptible rice cultivar Lemont and the resistant cultivar H₄/CODF, inoculated by the rice grain/hull method, Crowley, LA, 1996.

Rice genotype	Disease rating range	Number of plants	Mean disease rating	Standard error
Lemont	6-9 ^x	36	8.0 a ^y	1.18
H ₄ /CODF	1-4	36	3.0 b	0.90
H ₄ /CODF x Lemont (F_1)	1-3	36	2.5 b	0.53
Lemont x H ₄ /CODF (F_1)	1-3	22	2.5 b	0.71

^x Disease rating based on 0-9 scale, where 0 = no disease and 9 = plant dead or collapsed at maturity.

^y Means within columns followed by the same letter are not significantly different at the 0.05 level, according to Duncan's multiple range test.

The distributions of plant ShB reactions of reciprocal F_2 populations from crosses between resistant H₄/CODF and Lemont were continuous, but skewed to the resistant side (Figure 3). F_2 plants from the H₄/CODF x Lemont cross had a disease range from 0 to 9 with the mean rating of 3.7, while disease ratings of F_2 plants from the Lemont x H₄/CODF cross varied from 1 to 9 with a mean of 3.7. Both rating means were larger than that of the reciprocal F_1 populations, but close to that of the resistant parent. Again, this verified the dominant nature of this partial resistance. Based on the distribution patterns of F_2 plant ratings and disease rating ranges of both parents, the boundaries between resistance and susceptibility were set at 5 for both F_2 populations. The chi-square test showed that F_2 progeny for both reciprocal crosses fit a 3:1 resistant:susceptible segregation ratio. In 1997, an independently generated F_2 population of H₄/CODF x Lemont was tested using the same inoculation method and by the rice straw inoculation method (Chapter 2). Although the disease was not as severe as that in 1996, similar distribution patterns were observed (Figure 4). The data also fit a 3:1

resistant:susceptible ratio with probabilities of 0.20 and 0.10, respectively. Thus, partial resistance in H₄/CODF was controlled by one dominant gene.

The distribution of sheath blight ratings of backcross populations is shown in Figure 5. None of 43 plants from the backcross (H₄/CODF x Lemont) x H₄/CODF fell into the susceptible category. This further verified that partial ShB resistance in H₄/CODF was a dominant character. However, 42 plants from the backcross between the F₁ and the susceptible parent segregated in a 1:1 resistant:susceptible ratio (25:17), as would be expected for a single gene controlled character.

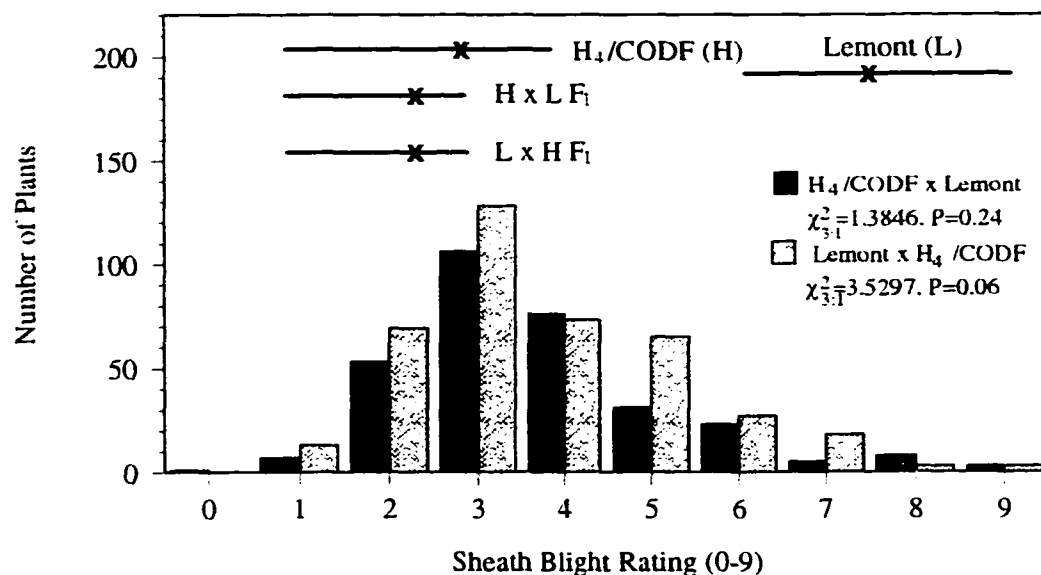


Figure 3. Distribution of sheath blight ratings (0-9) of plants in F₂ populations from reciprocal crosses between the sheath blight susceptible rice cultivar Lemont and the resistant cultivar H₄/CODF, inoculated by the rice grain/hull method, Crowley, LA, 1996.

The hypothesis of a single dominant gene for partial ShB resistance in H₄/CODF was further tested by evaluating F₃ lines derived from randomly collected F₂ plants from

the population of H₄/CODF x Lemont. As predicted by the hypothesis, data from the F₃ lines fit a 1:2:1 resistant:segregating:susceptible ratio (Table 11). Overall, the results from F₁, F₂, BC₁, and F₃ populations confirmed that most portion of partial ShB resistance in H₄/CODF appeared to be controlled by a single dominant gene.

3.3.2. INHERITANCE OF PARTIAL SHEATH BLIGHT RESISTANCE FROM LB86-30344

Significant differences in ShB rating were found between the susceptible parent cultivar Lemont and the resistant line LB86-30344. However, no significant differences were detected between the two reciprocal F₁ populations or the F₁ populations and the resistant parent (Table 12). So, the partial ShB resistance in LB86-30344 was also a dominant character, which was further verified by the skewed distribution of F₂ populations toward resistant side (Figure 6). Maternal effects were not significant.

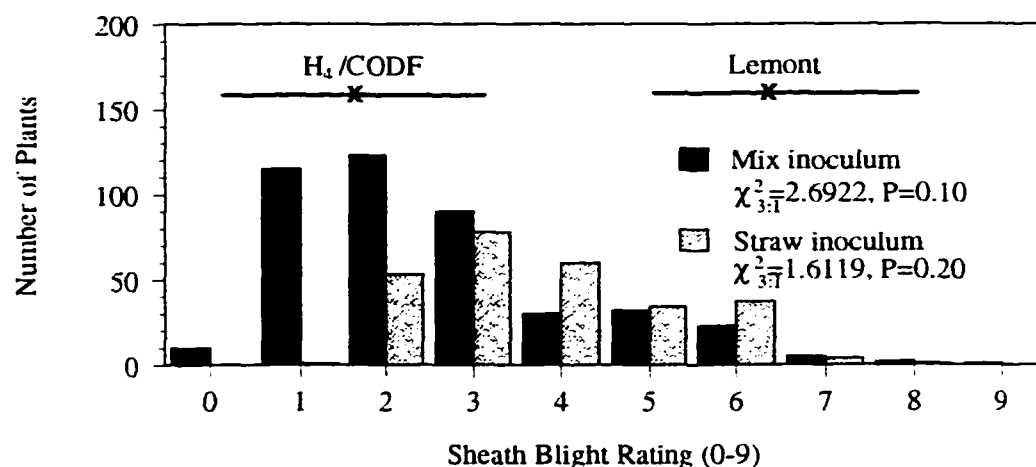


Figure 4. Distribution of sheath blight ratings (0-9) of F₂ plants in two sets of F₂ plants from the same population from a cross between the sheath blight susceptible rice cultivar Lemont and the resistant cultivar H₄/CODF when inoculated by the rice grain/hull and rice straw methods, Crowley, LA, 1997.

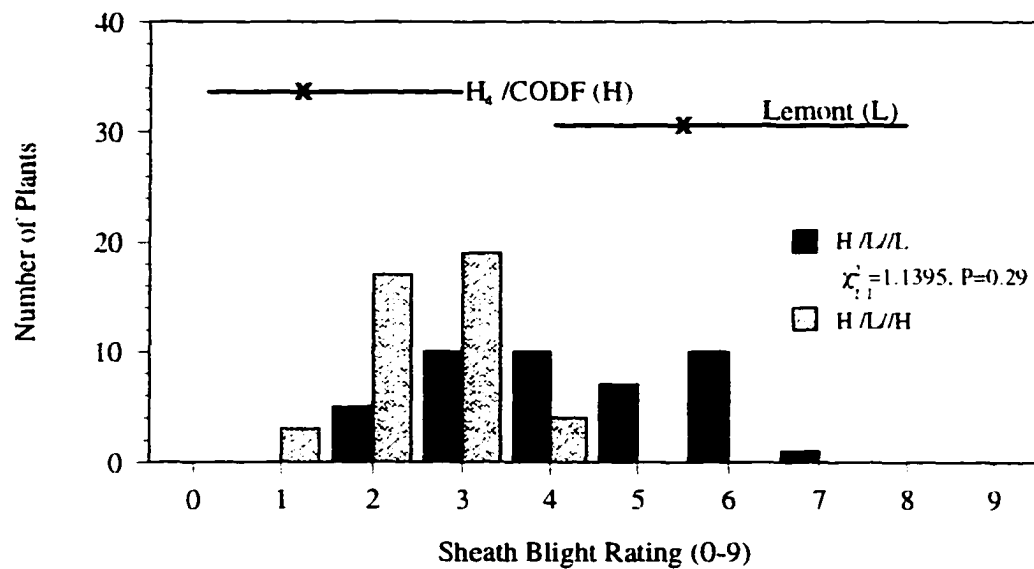


Figure 5. Distribution of sheath blight ratings (0-9) of plants from the BC₁F₁ populations of the crosses (H₄/CODF x Lemont) x Lemont and (H₄/CODF x Lemont) x H₄/CODF, inoculated by the rice grain/hull method, Crowley, LA, 1997.

Table 11. Sheath blight reaction of F₃ lines derived from single F₂ plants from the H₄/CODF x Lemont cross, inoculated by the rice grain/hull method, Crowley, LA, 1997.

Resistant lines ^a	Segregating lines	Susceptible lines	Total
35	51	19	105

$\chi^2_{1:2:1} = 4.9619, P=0.08.$

^a Resistant lines rated 5 or less and susceptible lines rated 6 or more on the 0-9 rating scale.

Table 12. Sheath blight reaction of parents and the F_1 generations from reciprocal crosses between the susceptible rice cultivar Lemont and the resistant line LB86-30344, inoculated by the rice grain/hull method, Crowley, LA, 1995.

Rice genotype	Disease rating range	Number of plants	Mean disease rating	Standard error
Lemont	6-9 ^x	36	7.5 a ^y	1.11
LB86-30344	0-4	36	2.3 b	0.90
LB86-30344 x Lemont (F_1)	0-4	28	1.8 b	1.04
Lemont x LB86-30344 (F_1)	0-4	24	2.0 b	0.91

^x Disease rating based on 0-9 scale, where 0 = no disease, 9 = plant dead or collapsed at maturity.

^y Means within a column followed by the same letter are not significantly different at the 0.05 level, according to Duncan's multiple range test.

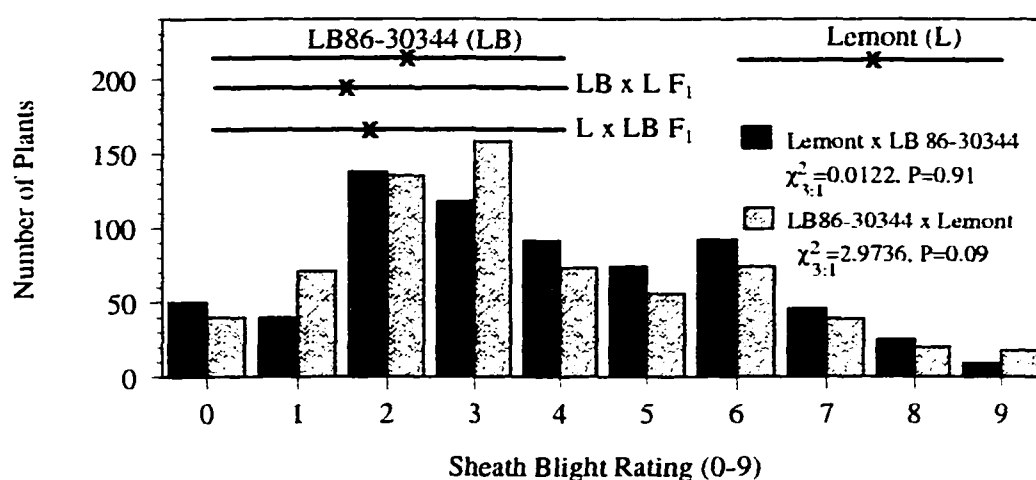


Figure 6. Distribution of sheath blight ratings (0-9) of plants in F_2 populations from reciprocal crosses between the sheath blight susceptible rice cultivar Lemont and the resistant line LB86-30344, inoculated by the rice grain/hull method, Crowley, LA, 1995.

Plants for both reciprocal F_2 populations showed a bimodal distribution (Figure 6). Based on this distribution, the boundary between resistant and susceptible was set at the 5 rating. The resistant to susceptible ratio for the population of Lemont x LB86-30344 was 511 resistant:172 susceptible, and 531 resistant:151 susceptible for the reciprocal cross LB86-30344 x Lemont. Chi-square tests showed that both populations

fit a 3:1 segregation ratio with probabilities of 0.91 and 0.09, respectively. Thus, the partial ShB resistance in LB86-30344 also appeared to be controlled by a single dominant gene. This hypothesis was further verified by F_3 lines derived from randomly collected F_2 plants from the LB86-30344 x Lemont cross (Table 13). One hundred and twenty tested F_3 lines segregated in a 1:2:1 resistant:segregating:susceptible ratio which was expected for a single dominant character.

Table 13. Sheath blight reaction of F_3 lines derived from single F_2 plants from the cross LB86-30344 x Lemont, inoculated by the rice grain/hull method, Crowley, LA, 1996.

Resistant lines ^a	Segregating lines	Susceptible lines ^a	Total
30	63	27	120

$\chi^2_{1:2:1} = 0.40, P=0.82.$

^a Resistant lines rated 5 or less and susceptible lines rated 6 or more on the 0-9 rating scale.

3.3.3. INHERITANCE OF PARTIAL SHEATH BLIGHT RESISTANCE FROM JASMINE 85

Both reciprocal F_1 populations and plants of the resistant parent Jasmine 85 had similar ShB ratings, which were significantly different from that of the susceptible cultivar Lemont (Table 14). So the partial resistance to ShB in the cultivar Jasmine 85 also was a dominant character. The skewed distribution of F_2 plants to the resistant side of the F_2 population and the lack of segregation in the backcross population from the cross between the F_1 and the resistant parent further verified this hypothesis (Figures 7 and 8). Comparison of disease ratings of both reciprocal F_1 populations showed that no significant maternal effects were detected. Compared to the parents, the two reciprocal

F₁ populations had less variation in ShB ratings, which may be attributed to wider spacing due to transplanting.

Plants in the F₂ population showed a continuous distribution of disease ratings, but skewed toward the resistant parent's rating (Figure 7). The valley of this distribution, which was at rating 4, was used as the boundary for dividing resistant and susceptible plants. The data (549 resistant:189 susceptible) fit a 3:1 resistant:susceptible ratio with a probability of 0.70. So the partial resistance to ShB in Jasmine 85 also was controlled by a single dominant gene.

None of the 31 plants tested from the backcross between the F₁ and the resistant parent showed segregation for their ShB reaction, while 72 plants from the backcross between the F₁ and the susceptible parent segregated in a 1:1 resistant:susceptible ratio (42:30) with a probability of 0.16 (Figure 8). This verified the hypothesis drawn from the disease reactions of the F₂ plants that a single dominant gene controlled the partial ShB resistance in Jasmine 85.

Table 14. Sheath blight reaction of parents and the F₁ generations from reciprocal crosses between the susceptible rice cultivar Lemont and the resistant cultivar Jasmine 85, inoculated by the rice grain/hull method, Crowley, LA, 1995.

Rice genotype	Disease rating range	Number of plants	Mean disease rating	Standard error
Lemont	5-9 ^x	36	6.7 a ^y	1.23
Jasmine 85	0-5	36	2.8 b	1.16
Jasmine 85 x Lemont (F ₁)	2-4	36	2.7 b	0.55
Lemont x Jasmine 85 (F ₁)	2-3	28	2.6 b	0.52

^x Disease rating based on 0-9 scale, where 0 = no disease, 9 = plant dead or collapsed at maturity.

^y Means within columns followed by the same letter are not significantly different at the 0.05 level, according to Duncan's multiple range test.

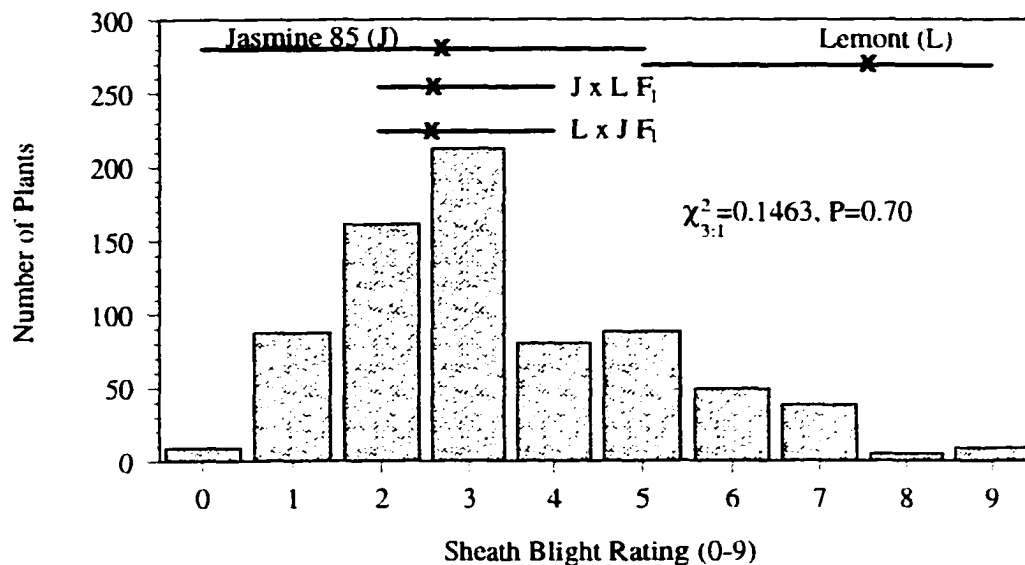


Figure 7. Distribution of sheath blight ratings (0-9) of F₂ plants in the population from a cross between the sheath blight susceptible rice cultivar Lemont and the resistant cultivar Jasmine 85, inoculated by the rice grain/hull method, Crowley, LA, 1995.

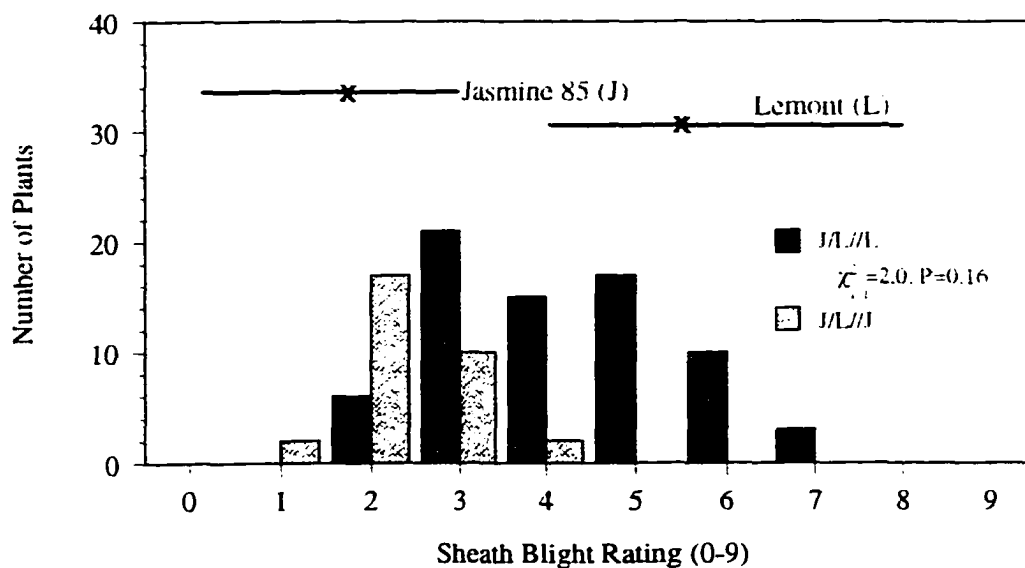


Figure 8. Distribution of sheath blight ratings (0-9) of plants from BC₁F₁ populations of the crosses (Jasmine 85 x Lemont) x Lemont and (Jasmine 85 x Lemont) x Jasmine 85, inoculated by the rice grain/hull method, Crowley, LA, 1997.

The single gene hypothesis was further verified by the ShB reactions of the F_1 and bulked F_4 ($F_{2,4}$) lines derived from F_2 plants of the Jasmine 85 x Lemont cross (Table 15). One hundred and twenty F_3 lines segregated into three groups with 35 lines being homozygous resistant, 60 segregating, and 25 homozygous susceptible. The data fit a 1:2:1 ratio which was expected for single gene segregation in the F_1 with a probability of 0.64. The data from bulked F_4 ($F_{2,4}$) lines also fit the 1:2:1 ratio with a probability of 0.29 (Table 15).

Table 15. Sheath blight reaction of $F_{2,3}$ and $F_{2,4}$ lines derived from single F_2 plants from the Jasmine 85 x Lemont cross, inoculated by the rice grain/hull method, Crowley, LA, 1996-97.

Source	Resistant ^a	Segregating	Susceptible ^a	Total	χ^2 value	<i>P</i> value
$F_{2,3}$ lines	35	60	25	120	1.67	0.64
$F_{2,4}$ lines	18	37	11	66	2.45	0.29

^a Resistant lines rated 5 or less and susceptible lines rated 6 or more on the 0-9 rating scale.

3.3.4. INHERITANCE OF PARTIAL SHEATH BLIGHT RESISTANCE FROM TEQING

Sheath blight reactions of the parents and the F_1 generations from the reciprocal crosses between the susceptible rice cultivar Lemont and the resistant cultivar Teqing are shown in Table 16. Lemont had disease ratings ranging from 5 to 8 with a mean of 6.5. Teqing had disease ratings that ranged from 1 to 5 with a mean of 2.9. Mean disease ratings for both reciprocal cross F_1 populations were lower than, but not significantly different from that of the resistant parent. The partial ShB resistance in Teqing was also major gene and apparently controlled by a single dominant gene. This was verified by the skewed distribution of ShB ratings toward that of the resistant parent in the F_2

population (Figure 9). There was no significant difference between mean ShB ratings of the two reciprocal F_1 populations, or these populations and Teqing. Maternal effects were not important for partial ShB resistance in Teqing.

Table 16. Sheath blight reaction of parents and the F_1 generations from reciprocal crosses between the susceptible rice cultivar Lemont and the resistant cultivar Teqing, inoculated by the rice grain/hull method, Crowley, LA, 1995.

Rice genotype	Disease rating range	Number of plants	Mean disease rating	Standard error
Lemont	5-8 ^x	36	6.5 a ^y	1.09
Teqing	1-5	36	2.9 b	1.02
Teqing x Lemont (F_1)	0-5	36	2.2 b	0.96
Lemont x Teqing (F_1)	0-4	29	2.6 b	0.83

^x Disease rating based on 0-9 scale, where 0 = no disease, 9 = plant dead or collapsed at maturity.

^y Means within columns followed by the same letter are not significantly different at the 0.05 level, according to Duncan's multiple range test.

The distribution of 517 F_2 plants from this cross showed a bimodal distribution (Figure 9). The data fit a 3:1 resistant:susceptible ratio (387:130) with a probability of 0.94. A single dominant gene controlled the partial ShB resistance in Teqing. The effect of this major gene as estimated by the difference between the mean of the resistant F_2 plants and the mean of the susceptible F_2 plants was about 3.2 points on the 0-9 rating scale. One hundred and twenty F_3 lines derived from randomly collected F_2 plants of the Lemont x Teqing cross segregated in a 1:2:1 resistant:segregating:susceptible ratio which was expected for single gene segregation (Table 17).

Table 17. Sheath blight reaction of F₃ lines derived from single F₂ plants from the Lemont x Teqing cross, inoculated by the rice grain/hull method, Crowley, LA, 1996.

Resistant lines ^a	Segregating lines	Susceptible lines ^a	Total
37	55	28	120

$\chi^2_{1:2:1} = 2.8667, P=0.19.$

^a Resistant lines rated 5 or less and susceptible lines rated 6 or more on the 0-9 rating scale.

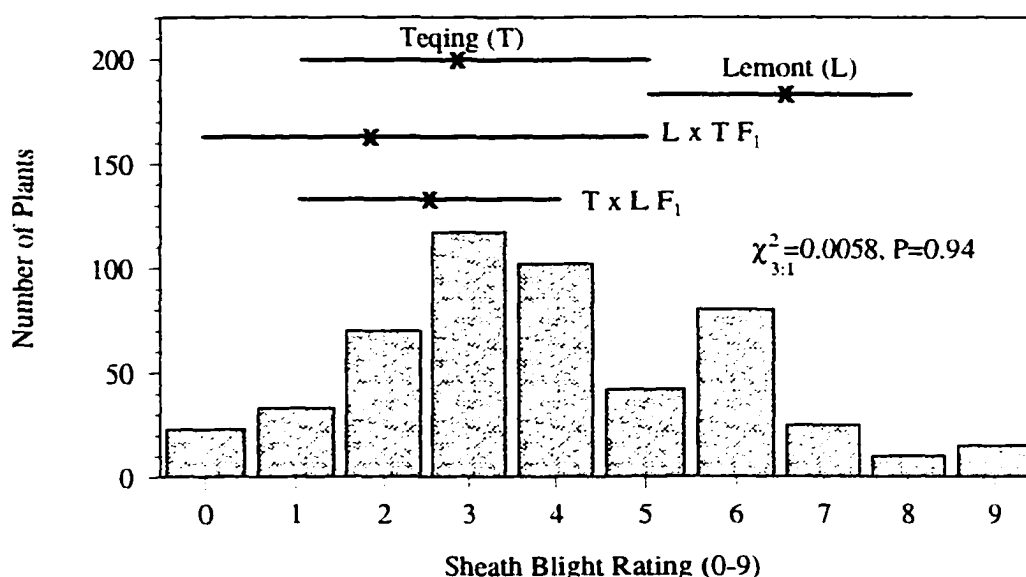


Figure 9. Distribution of sheath blight ratings (0-9) of F₂ plants in F₂ population from a cross between the sheath blight susceptible rice cultivar Lemont and the resistant cultivar Teqing, inoculated by the rice grain/hull method, Crowley, LA, 1995.

3.3.5. INHERITANCE OF PARTIAL SHEATH BLIGHT RESISTANCE FROM GUI CHAO

Reciprocal F₁ populations showed a resistant reaction similar to that of the resistant parent Gui Chao, which indicated that inheritance of the partial ShB resistance was dominant (Table 18). The similar reaction in the reciprocal F₁ populations indicated that no significant cytoplasmic factors were involved in expression of partial ShB

resistance in Gui Chao. The mean disease ratings for the F_1 populations and Gui Chao were not significantly different.

Table 18. Sheath blight reaction of parents and the F_1 generations from reciprocal crosses between the susceptible rice cultivar Lemont and the resistant cultivar Gui Chao, inoculated by the rice grain/hull method, Crowley, LA, 1996.

Rice genotype	Disease rating range	Number of plants	Mean disease rating	Standard error
Lemont	5-9 ^x	36	7.5 a ^y	0.90
Gui Chao	0-4	35	3.0 b	0.81
Gui Chao x Lemont (F_1)	0-3	24	2.7 b	0.79
Lemont x Gui Chao (F_1)	0-3	20	2.5 b	0.68

^x Disease rating based on 0-9 scale, where 0 = no disease, 9 = plant dead or collapsed at maturity.

^y Means within columns followed by the same letter are not significantly different at the 0.05 level, according to Duncan's multiple range test.

Plants for the reciprocal F_2 populations showed a bimodal distribution (Figure 10). Based on this distribution, the boundary between resistant and susceptible was set at rating 4 for Lemont x Gui Chao and at rating 5 for Gui Chao x Lemont. For the Lemont x Gui Chao population, 238 F_2 plants segregated as 170 resistant and 68 susceptible. A chi-square test showed that the data fit a 3:1 resistant:susceptible ratio with the probability of 0.20 which was expected for the segregation of a single dominant gene. However, for the Gui Chao x Lemont cross, the segregation of 575 F_2 plants did not fit a 3:1 resistant:susceptible ratio. More susceptible plants were observed than expected, which may be due to the maternal effects or thick stand or higher disease pressure.

Classification of 120 F_3 lines resulted in 28 homozygous resistant lines, 54 segregating lines, and 38 susceptible lines, which fit a 1:2:1 F_3 genotypic ratio with a probability of 0.19 (Table 19). This supported the hypothesis that Gui Chao had a single dominant gene for partial ShB resistance.

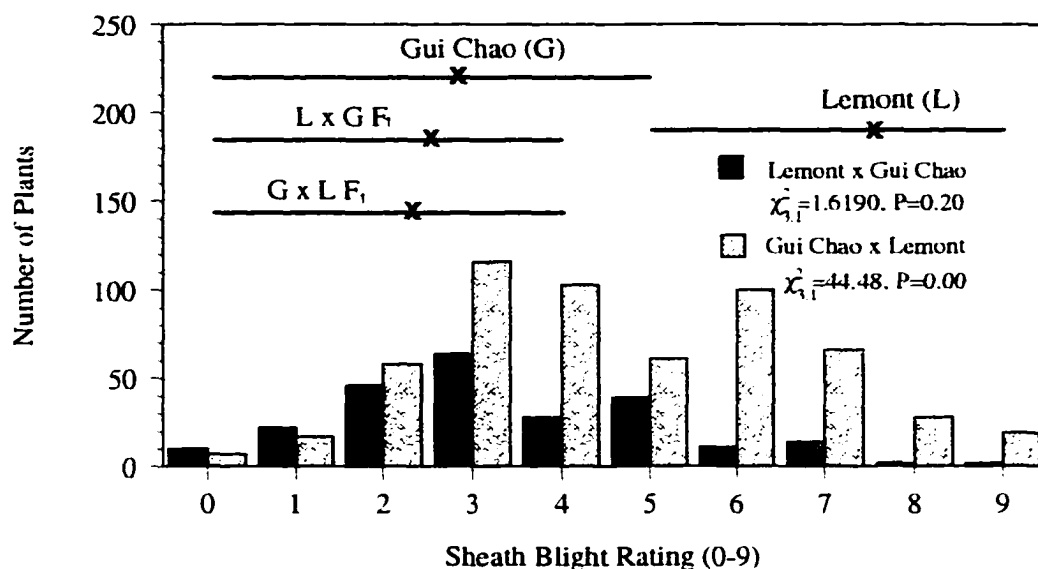


Figure 10. Distribution of sheath blight ratings (0-9) of F_2 plants in F_2 populations from reciprocal crosses between the sheath blight susceptible rice cultivar Lemont and the resistant cultivar Gui Chao, inoculated by the rice grain/hull method, Crowley, LA, 1995.

Table 19. Sheath blight reaction of F_3 lines derived from single F_2 plants from the Gui Chao x Lemont cross, Crowley, LA, 1996.

Resistant lines ^a	Segregating lines	Susceptible lines ^a	Total
28	54	38	120

$$\chi^2_{1:2:1} = 2.8667, P=0.19.$$

^a Resistant lines rated 5 or less and susceptible lines rated 6 or more on the 0-9 rating scale.

3.3.6. INHERITANCE OF PARTIAL SHEATH BLIGHT RESISTANCE FROM YANGDAO 4

The mean disease ratings of Lemont, Yangdao 4, and F_1 plants from the reciprocal crosses were 6.8, 3.6, 3.2, and 2.9, respectively (Table 20). The F_1 reactions indicated that partial ShB resistance in Yangdao 4 was dominant, and no significant maternal effects were involved in controlling the partial ShB resistance. Means of the F_1 disease ratings and Yangdao 4 were not significantly different. The F_2 population from

the Yangdao 4 x Lemont cross showed a bimodal distribution, however, the F_2 population from the Lemont x Yangdao 4 cross showed a continuous distribution (Figure 11). When the boundaries between resistant and susceptible were set at 4, both populations segregated in a 9:7 ratio with probabilities of 0.14 and 0.77, respectively, which indicated that two dominant genes with complementary interaction apparently controlled the partial ShB resistance in Yangdao 4.

Table 20. Sheath blight reaction of parents and the F_1 generations from reciprocal crosses between the susceptible rice cultivar Lemont and the resistant cultivar Yangdao 4, inoculated by the rice grain/hull method, Crowley, LA, 1996.

Rice genotype	Disease rating range	Number of plants	Mean disease rating	Standard error
Lemont	6-9 ^x	36	6.8 a ^y	1.29
Yangdao 4	2-5	36	3.6 b	1.12
Yangdao 4 x Lemont (F_1)	2-5	26	3.2 b	0.94
Lemont x Yangdao 4 (F_1)	2-4	29	2.9 b	0.83

^x Disease rating based on 0-9 scale, where 0 = no disease, 9 = plant dead or collapsed at maturity.

^y Means within columns followed by the same letter are not significantly different at the 0.05 level, according to Duncan's multiple range test.

3.3.7. GENETIC ANALYSIS OF PARTIAL SHEATH BLIGHT RESISTANCE OF F_3 AND $F_{2,4}$ LINES FROM THE JASMINE 85 x LEMONT, TEQING x LEMONT, AND LB86-30344 x LEMONT CROSSES

The parent-offspring correlation coefficients are shown in Table 21. Regardless of cross, the highest correlation coefficient was observed between F_3 and $F_{2,4}$. This further supports the hypothesis that partial ShB resistance is an inheritable character and can be easily traced from generation to generation under uniform test conditions. The correlations also were strong between F_2 and F_3 , and between F_2 and $F_{2,4}$ for all crosses except for Teqing x Lemont. The small sample size of the Teqing x Lemont cross may

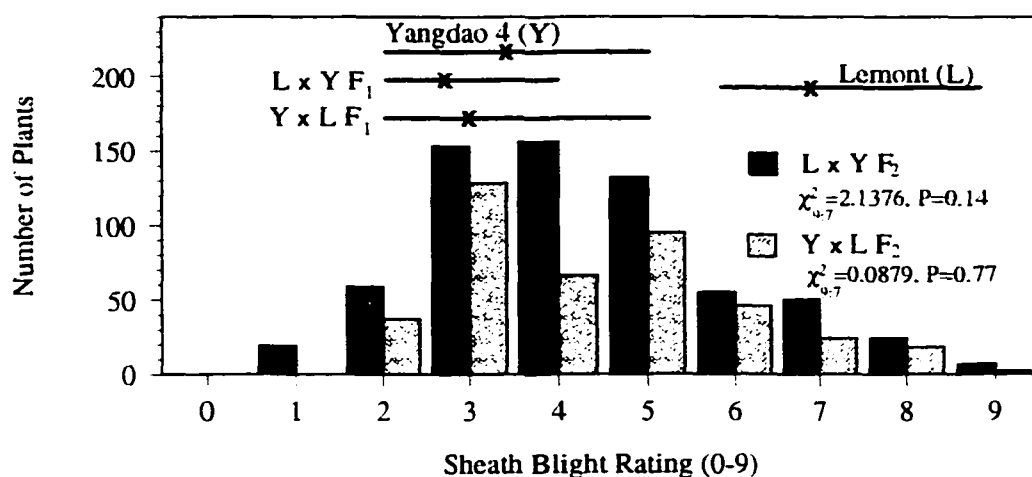


Figure 11. Distribution of sheath blight ratings (0-9) of F₂ plants in F₂ populations from reciprocal crosses between the sheath blight susceptible rice cultivar Lemont and the resistant cultivar Yangdao 4, Crowley, LA, 1996.

Table 21. Pearson's correlation analysis of sheath blight ratings of F₂, F₃, and F_{2,4} progenies for the Jasmine 85 (JA 85) x Lemont, Teqing x Lemont, and LB86-30344 (LB86) x Lemont crosses, inoculated by the rice grain/hull method, Crowley, LA, 1997.

Cross	Number of lines	Generation	Pearson's correlation coefficient by	
			F ₃	F _{2,4}
JA 85 x Lemont	50	F ₂ ^a	0.45** ^b	0.33**
		F ₃		0.79**
Teqing x Lemont	16	F ₂	0.25	-0.11
		F ₃		0.71**
LB86 x Lemont	64	F ₂	0.39**	0.34**
		F ₃		0.72**

^a F₂ rating was taken in 1996 based on 0-9 rating scale, where 0 = no disease, 9 = plant dead or collapsed at maturity.

^b *, ** significant at the 0.05 and 0.01 level, respectively.

have resulted in the low correlation coefficient. The reduction of correlation coefficient from F₂:F₃ to F₂:F_{2,4} may contribute to the dominant effect of partial ShB resistance in these two resistant genotypes, which further supports the dominant character hypothesis

drawn from the F_1 and F_2 data (Mather and Jinks, 1982). Because F_2 : $F_{2,4}$ and F_3 : $F_{2,4}$ were tested at different times, the difference in disease pressure in the two environments may have caused the low correlation between F_2 and F_3 , and between F_2 and $F_{2,4}$ compared to the high correlation between F_3 and $F_{2,4}$. This suggests that the partial ShB resistance is environment sensitive. To select for ShB resistance, a controlled test or evaluation is needed.

The broad-sense heritabilities estimated by F_3 and $F_{2,4}$ lines are listed in Table 22. The high heritabilities (more than 70%) observed in the Jasmine 85 x Lemont and LB86-30344 x Lemont crosses, coupled with the bimodal distribution of ShB ratings for F_2 plants, also was an indication of major gene resistance (Pang and Halloran, 1996a). The ShB resistance from these two crosses had similar broad-sense heritabilities, which suggests that the two resistant genotypes share the same resistance mechanism or a similar genetic background. The low heritability of ShB resistance in the Teqing x Lemont cross may be due to the small number of F_3 and $F_{2,4}$ lines tested.

Major gene effects estimated by the difference between the mean of resistant F_2 plants and the mean of susceptible F_2 plants (Jiang et al., 1994) are listed in Table 23, which range from 2.7 to 4.8 rating scale points. The difference between reciprocal crosses may be due to the effect of genetic background. Major gene effects account for more than 56% of the phenotypic variation in six genotypes. These results indicate that a high level of partial ShB resistance may be achieved by combining and incorporating the major resistance genes into commercial rice cultivars.

Table 22. Broad-sense heritability estimated for sheath blight resistance of F_3 and $F_{2:4}$ lines from the Jasmine 85 (JA 85) x Lemont, Teqing x Lemont, and LB86-30344 (LB86) x Lemont crosses.

Cross	Number of lines	Broad-sense heritability estimated by	
		F_3	F_4
JA 85 x Lemont	50	73.2%	79.3%
Teqing x Lemont	16	59.5%	51.2%
LB86 x Lemont	64	74.0%	82.1%

Table 23. Segregation for resistance to sheath blight caused by *Rhizoctonia solani* Kühn in rice in F_2 populations for crosses between six resistant genotypes and the susceptible cultivar Lemont, Crowley, LA, 1995-1996.

Pedigree	Resistant		Susceptible		Major gene effects
	Number of plants	Mean rating	Number of plants	Mean rating	
H ₄ /CODF x Lemont	243	3.0 ^a	70	6.0	3.0 ^b
Lemont x H ₄ /CODF	283	2.9	116	5.7	2.8
LB86-30344 x Lemont	543	2.6	141	7.4	4.8
Lemont x LB86-30344	511	2.7	172	6.7	4.0
Jasmine 85 x Lemont	549	2.5	189	5.9	3.4
Teqing x Lemont	387	3.5	130	6.7	3.2
Gui Chao x Lemont	362	3.6	213	6.8	3.2
Lemont x Gui Chao	170	2.7	68	5.8	3.1
Yangdao 4 x Lemont	231	3.1	185	5.8	2.7
Lemont x Yangdao 4	387	3.2	268	6.0	2.8

^a Disease rating based on 0-9 scale, where 0 = no disease, 9 = plant dead or collapsed at maturity.

^b Difference between the mean of resistant plants and the mean of susceptible plants.

3.4. DISCUSSION

Sheath blight is a devastating disease of rice worldwide (Rao, 1995; Lee and Rush, 1983). The efforts of breeding for resistance to sheath blight were greatly hindered by the lack of complete resistance (Dasgupta, 1992). Many controversies remain on the nature of genetic resistance to ShB, even though the fact that large variation in reaction to ShB exists in rice germplasm is widely accepted by many rice breeders and

pathologists (Li et al., 1995; Xie et al., 1990; Rao, 1995, Peng et al., 1986). All rice genotypes can be infected by *R. solani* under favorable weather conditions, and water-soaked lesions typical of a susceptible reaction will appear shortly after infection (Ou, 1985; Dath, 1990). Sheath blight resistance is mainly expressed in the form of low disease incidence, small lesion size, fewer lesion numbers, and slow vertical development (low RLH% and rating), which should be considered as partial resistance (Groth and Nowick, 1992; Dath, 1990; Xie et al., 1990).

Parlevliet (1978, 1979, 1989) defined partial resistance as a form of incomplete resistance in which the individual lesions are characterized by a susceptible infection type and which is controlled by minor genes whose effects are too small to detect individually. Although this general definition of partial resistance was widely accepted by plant breeders and pathologists, the argument that partial resistance was controlled by minor genes was challenged by different researchers with different crop-pathogen systems (Kolmer, 1996; Rubiales and Niks, 1995; Concibido et al., 1996; Keri et al., 1997; Ori et al., 1997; Colon et al., 1995; Pang and Halloran, 1996; Caranta and Palloix, 1996). After a detailed study of the major gene *Lr34* for resistance to leaf rust in wheat, Rubiales and Niks (1995) revealed that the resistance caused by *Lr34* fits Parlevliet's definition of partial resistance. As a consequence, *Lr34* demonstrated that partial resistance in wheat to leaf rust was controlled by a single major gene. Colon et al. (1995) studied the partial resistance to late blight in potato, and revealed that besides minor genes, several major genes also contribute to the partial resistance in wild species and cultivated cultivars. Cargeeg (1980) proposed that the incomplete blackleg resistance in rapeseed may be

determined by the combined effects of major and minor genes. This type of genetic control of resistance has also been reported for northern leaf blight resistance in maize by various workers (Ullstrup and Brunson, 1947; Leonard, 1974; Hamid et al., 1982). In rice, plant height and amylose content are controlled by one or a few major genes and modified by minor genes (Jiang et al., 1994).

In this study, six parents all showed partial resistance to *R. solani* isolate LR172. Similar disease reactions were observed between the F_1 populations of reciprocal crosses and the resistant parent for all crosses, which suggests that the partial ShB resistance was a dominant character. The dominant hypothesis also was confirmed by the distribution of disease ratings in the F_2 and BC_1 populations. Hashioka (1951a) first reported that moderate ShB resistance could be dominant. Several other studies with different resistance sources also indicated that partial ShB resistance may be dominant or partially dominant (Masajo, 1976; Goita, 1984; Pan et al., 1996). Marchetti and McClung (1994) found the distribution of ShB ratings of F_3 families for the RU8703196/Rosemont cross was skewed towards resistance, and this may also indicate that ShB resistance in RU8703196 was dominant. Maternal effects were not significant in any parent evaluated in this study. The same result was reported by Marchetti and McClung (1994) for the elite ShB resistant line RU8703196.

Genetic analysis of segregating F_2 populations derived from crosses between the susceptible cultivar Lemont and resistant parents revealed that the expected 3:1 resistant:susceptible ratio in the F_2 generations was demonstrated for all parents except Yangdao 4. This was confirmed by evaluation of F_3 or $F_{2.4}$ lines and BC_1 populations.

Therefore, H₄/CODF, LB86-30344, Jasmine 85, Teqing, and Gui Chao each have one dominant gene for resistance to sheath blight. Plants of F₂ populations for the reciprocal crosses between Yangdao 4 and Lemont segregated in a 9:7 resistant:susceptible ratio, which suggested that two complementary dominant genes may control the partial ShB resistance in Yangdao 4. The continuous distributions of ShB ratings in the F₂ populations may be due in part to the effects of minor genes and in part to the effects of the environment on disease development. The partial ShB resistance may be controlled by the combined effects of both major and minor genes.

The highly significant correlations observed between F₃ and F_{2,4} lines for the crosses Jasmine 85 x Lemont, Teqing x Lemont, and LB86-30344 x Lemont indicated that partial ShB resistance was heritable and easily traced from generation to generation under uniform test conditions. The correlations between F₂ and F₃, and between F₂ and F_{2,4} also were significant, but were much smaller than the correlations between F₃ and F_{2,4}, which indicated that partial ShB resistance was environment sensitive. For crosses Jasmine 85 x Lemont and LB86-30344 x Lemont, the higher broad-sense heritabilities estimated by F₃ and F_{2,4} lines, coupled with the bimodal distribution of ShB ratings for F₂ plants, was an indication of major gene resistance (Pang and Halloran, 1996a). The results of this study suggest that a high level of partial ShB resistance may be achieved by combining and incorporating the major resistance genes into commercial rice cultivars.

CHAPTER 4. ALLELIC RELATIONSHIPS AMONG MAJOR GENES CONTROLLING PARTIAL SHEATH BLIGHT RESISTANCE IN SEVEN RICE GENOTYPES

4.1. INTRODUCTION

Sheath blight (ShB), caused by *Rhizoctonia solani* Kühn, is one of the most destructive rice diseases in the southern United States (Lee and Rush, 1983). Breeding and utilization of resistant cultivars is the only practical and economic way to control this disease. Though only partial level ShB resistance is available, this type of resistance can offer adequate protection against the pathogen under field conditions (Li et al., 1995).

Historically, partial resistance to plant disease was widely believed to be polygenically inherited, but this argument has been challenged by different researchers using different plant-parasite systems (Kolmer, 1996; Rubiales and Niks, 1995; Colon et al., 1995; Pang and Halloran, 1996). In fact, partial resistance can be controlled by either major gene(s), combinations of major and minor genes, or by minor gene(s). Most of the genetic studies conducted on ShB resistance to date have shown that partial ShB resistance was controlled by one to three major genes. Hashioka (1951a, 1951b) first studied the inheritance of ShB resistance. Based on the segregation ratios of F_2 plants of six crosses between five resistant and three susceptible cultivars, it was proposed that Boera Ropo had two dominant genes, while Davao, Boenar, Asse Banda and one unnamed Chinese cultivar each had one dominant gene for resistance. Masajo (1976) reported that partial ShB resistance for the U.S. cultivars Zenith and Caloro was controlled by two pairs of partially dominant genes. Greenhouse tests showed that the partial ShB resistance in L201 and two breeding lines, RU7902185 and RU7902191,

was controlled by two complementary dominant genes (Goita, 1985; Hoff et al., 1984; Hoff et al. 1985). Recently, LSBR-5 and LSBR-33, two elite ShB resistant lines were developed through somaculture (Xie et al., 1990; Xie et al., 1992). The resistance in LSBR-5 was conferred by one recessive gene, while the resistance in LSBR-33 was conferred by two recessive genes. Some positive progress has been made in breeding resistant cultivars using those somaclonal variants (Rush et al., 1995; Rush et al., 1996). Preliminary tests also showed that the partial ShB resistance in the cultivars Teqing and Jasmine 85 was controlled by single dominant genes, and these two genes assorted independently of each other (Pan et al., 1995, 1996a, 1996b, and 1998).

Our previous studies (Chapter 3) showed that partial ShB resistance in H₄/CODF, LB86-30344, Jasmine 85, Teqing, and Gui Chao was controlled by single dominant genes, while the partial ShB resistance in Yangdao 4 was conferred by two complimentary dominant genes. However, it was not known whether the six parents possessed the same or different gene(s) for resistance. Lack of information on the identity of resistance genes present in cultivars or germplasm used in a breeding program may hinder the efficient use of the resistance genes. Therefore, identification and characterization of partial ShB resistance genes in rice cultivars or germplasm is an important prerequisite for the effective use of those genes in breeding for ShB resistance. Furthermore, all of these resistant parents have some unfavorable agronomic characters such as the tall plant height of LB86-30344 and H₄/CODF, the red pericarp of H₄/CODF, and pubescent foliage for all parent cultivars. To transfer partial resistance genes into commercial cultivars without introducing these unfavorable traits, information on the

linkage between partial ShB resistance and these unfavorable traits must be determined.

The objectives of this study were to determine if the resistant parents had common or different genes for partial ShB resistance, if these genes were known or unique, and if the partial ShB resistance was linked to unfavorable agronomic traits, such as tall plants, pubescent leaves, and red bran pigmentation.

4.2. MATERIALS AND METHODS

4.2.1. PLANT MATERIALS

Six resistant genotypes, H₄/CODF, LB86-30344, Jasmine 85, Teqing, Gui Chao, and Yangdao 4, were crossed with each other. The resistant parents also were crossed to the elite ShB resistant line LSBR-5 which possesses a single recessive gene for partial ShB resistance (Xie et al., 1992). Seeds harvested from F₁ plants grown in the greenhouse during the winter served as F₂ seeds to be tested in the field the next summer. The procedures for hybrid seed treatment, planting, and harvesting were the same as those described in Chapter 3. Reciprocal crosses were made for some parents, but were not planted in the F₂ because no significant difference was detected between the ShB resistance levels of reciprocal F₁ populations. About 100 individual F₂ plants were randomly harvested from the H₄/CODF x LB86-30344 and Teqing x Gui Chao crosses at maturity, and they were separately threshed and stored to be planted as F₃ lines the next year.

4.2.2. FIELD EXPERIMENTS

All experiments were conducted in field plots at the Louisiana State University Rice Research Station in Crowley, LA from 1995 to 1997.

Plants were grown in tiers of 2.4 m rows with a 25.4 cm spacing between rows. Plots of parents, F_2 , and F_3 generation plants were planted with a Hege 90 Series Drill Planter using 12-cell magazines. Each cell contains 50-60 seeds. However, greenhouse-grown seedlings of hybrids of F_1 populations were transplanted into the field after the permanent flood. Normal cultural practices were followed with plots receiving 16-47-47 (N- P_2O_5 - K_2O) kg/ha fertilizer drilled preplant and an additional 50 kg/ha N top-dressed at the green-ring stage. Plots were treated with propanil and bensulfuron methyl herbicides and carbofuran for rice water weevil control. After the permanent flood was applied, directly seeded plants were thinned or adjusted to 20-25 plants per row. Depending on seed availability for each generation in each year, the number of parental and F_1 plants evaluated was between 20 and 60, the number of F_2 plants was between 240 and 700, and the number of F_3 plants within each F_3 line was between 60 and 90.

4.2.3. INOCULATION AND DISEASE RATING

LR172, a highly-virulent *R. solani* isolate cultured on autoclaved 1:2 rice grain: hull mixture was used as inoculum in this test. Plants were inoculated at the maximum tillering stage with 50 ml of inoculum scattered over each row. Disease ratings were made on individual plants based on a 0-9 rating scale where 0 = no disease and 9 = plant dead and collapsed at maturity 30-35 days after heading (Rush et al., 1976). For each segregating F_2 population, the boundary between resistant and susceptible plants was determined by the pattern of the ShB rating distribution of that population and both parents. Individual plants of the F_3 lines also were scored and each line classified as homozygous resistant, segregating, or homozygous susceptible. In 1995, 247 F_2 plants of

the cross between the resistant line LB86-30344 and the susceptible cultivar Lemont were evaluated for ShB rating, leaf pubescence/glabrous, and plant height. Plant height was measured in centimeters from the base of the plant (soil line) to the collar of the flag leaf at maturity. Each of 200 F_2 individual plants from the H_4 /CODF x Lemont cross also was rated for ShB reaction and checked for bran color (red pericarp). The goodness of fit of the data to a specific genetic model was analyzed using the chi-square test.

4.3. RESULTS

4.3.1. GENETIC ANALYSIS OF CROSSES BETWEEN SHEATH BLIGHT RESISTANT PARENTS

Crosses between seven resistant parents were evaluated to determine whether resistance genes in these parents were different or common to each other. The F_1 progenies of all crosses between resistant parents were as resistant as their parents (Figures 12 to 23). However, this did not provide information on the allelic relationship of resistance genes, because resistance was dominant in six of the seven resistant parents.

Distribution of ShB ratings for plants in F_2 populations from the crosses between resistant parents are shown in Figures 12 through 23. The continuous distributions indicated that resistance to sheath blight was incomplete. All plants in the F_2 population of the cross LB86-30344 x H_4 /CODF were resistant, indicating that the resistance genes of LB86-30344 and H_4 /CODF were allelic (Figure 12). F_3 progenies derived from randomly harvested F_2 plants of this cross were grown and inoculated to verify the conclusions drawn from the study of the F_1 and F_2 populations. All 60 F_3 lines were homogeneous resistant, confirming that LB86-30344 and H_4 /CODF have the same

dominant gene for resistance. All plants in F_2 populations of from the crosses $H_4/CODF$ x Jasmine 85, Jasmine 85 x LB86-30344, and Gui Chao x Teqing showed a monomodal normal distribution (Figures 13, 14, and 15). In all three crosses, more than 95% of the F_2 plants were within the range of resistance of the parents. A few plants with disease ratings of 7 or 8 in the crosses $H_4/CODF$ x Jasmine 85 and Jasmine 85 x LB86-30344 were apparently present due to a mechanical seed mixture occurring during sampling or planting. The wide range of distribution may have been caused by the effects of minor or modifying genes, epistasis, or the interaction with environmental factors. The partial ShB resistance genes in $H_4/CODF$, Jasmine 85, and LB86-30344 were considered allelic, as were the resistance genes in Teqing and Gui Chao.

Segregation for susceptible F_2 progenies was observed in the crosses $H_4/CODF$ x Teqing, LB86-30344 x Teqing, and Jasmine 85 x Gui Chao (Figures 16, 17, and 18). The data from the last two crosses fit a 15:1 resistant:susceptible ratio with probabilities of 0.50 and 0.07, respectively, indicating that the resistance in Teqing and Gui Chao differs from that in $H_4/CODF$, LB86-30344, and Jasmine 85. These results also confirm our preliminary conclusions previously drawn from a study of the cross Teqing x Jasmine 85 that the resistance genes in these two parents were nonallelic (Pan et al., 1995, 1996a, 1996b, and 1998). Due to hot water damage, parent, F_1 , and F_2 populations from the cross $H_4/CODF$ x Teqing did not produce good stands and disease ratings were low. However, several F_2 plants showed susceptible reactions.

A bimodal distribution was observed in the crosses Jasmine 85 x LSBR-5 and LSBR-5 x Teqing (Figures 19 and 20). The data fit a 13:3 resistant:susceptible ratio with

probabilities of 0.19 and 0.18, respectively, indicating that the single recessive gene in LSBR-5 was not allelic to and assorted independently from the dominant genes in Jasmine 85 and Teqing.

Segregation in susceptible F_2 progenies also was observed in the crosses H_4 /CODF x Yangdao 4, Jasmine 85 x Yangdao 4, and Teqing x Yangdao 4 (Figures 21, 22, and 23), which indicated that the two complimentary dominant genes in Yangdao 4 were nonallelic to the dominant genes in H_4 /CODF, Jasmine 85, and Teqing. Segregation ratios were not calculated due to the small F_2 population size.

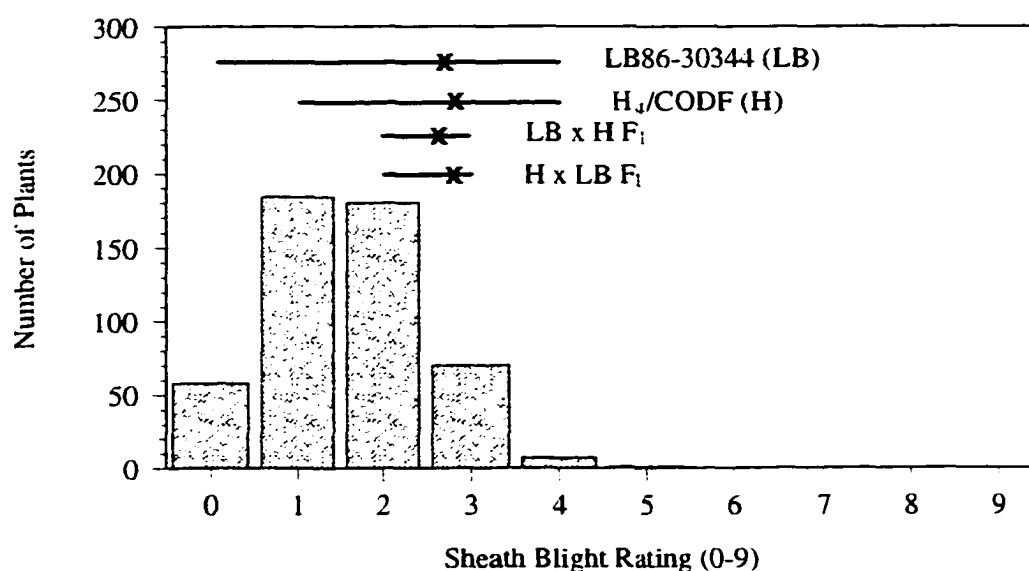


Figure 12. Distribution of sheath blight ratings (0-9) of F_2 plants inoculated by the rice grain/hull method in F_2 populations from a cross between the sheath blight resistant genotypes LB86-30344 and H_4 /CODF, Crowley, LA, 1996; lines show the rating ranges and x's mark the means for parent and F_1 populations.

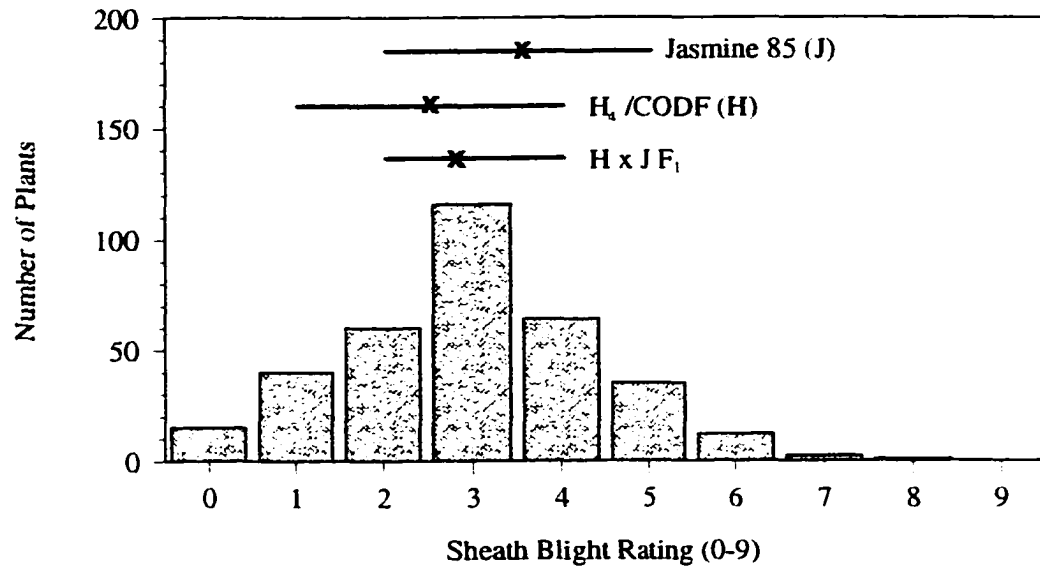


Figure 13. Distribution of sheath blight ratings (0-9) of F_2 plants inoculated by the rice grain/hull method in F_2 populations from a cross between the sheath blight resistant genotypes H_4 /CODF and Jasmine 85, Crowley, LA, 1996; lines show the rating ranges and x's mark the means for parent and F_1 populations.

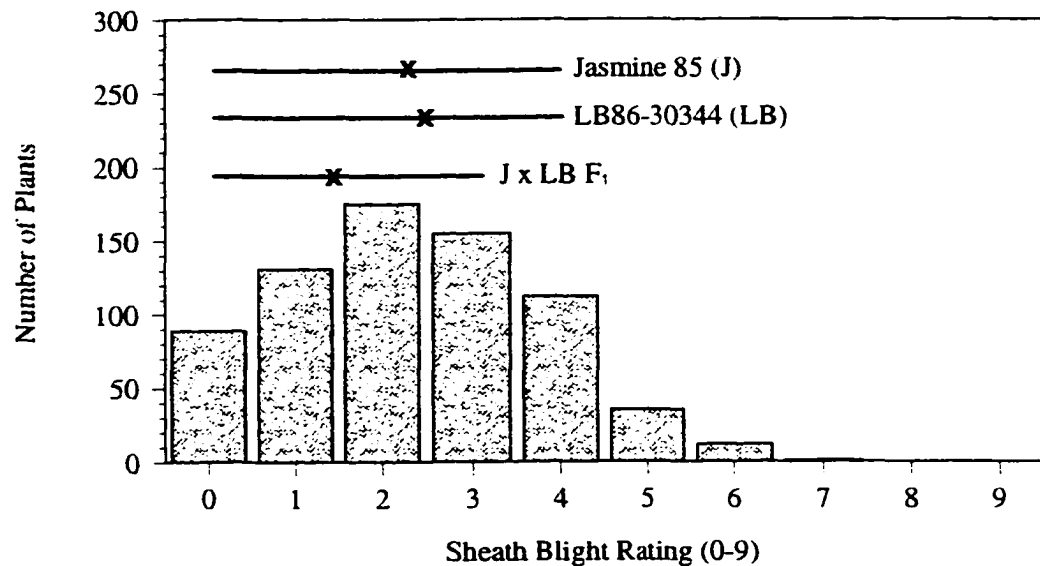


Figure 14. Distribution of sheath blight ratings (0-9) of F_2 plants inoculated by the rice grain/hull method in F_2 populations from a cross between the sheath blight resistant genotypes Jasmine 85 and LB86-30344, Crowley, LA, 1995; lines show the rating ranges and x's mark the means for parent and F_1 populations.

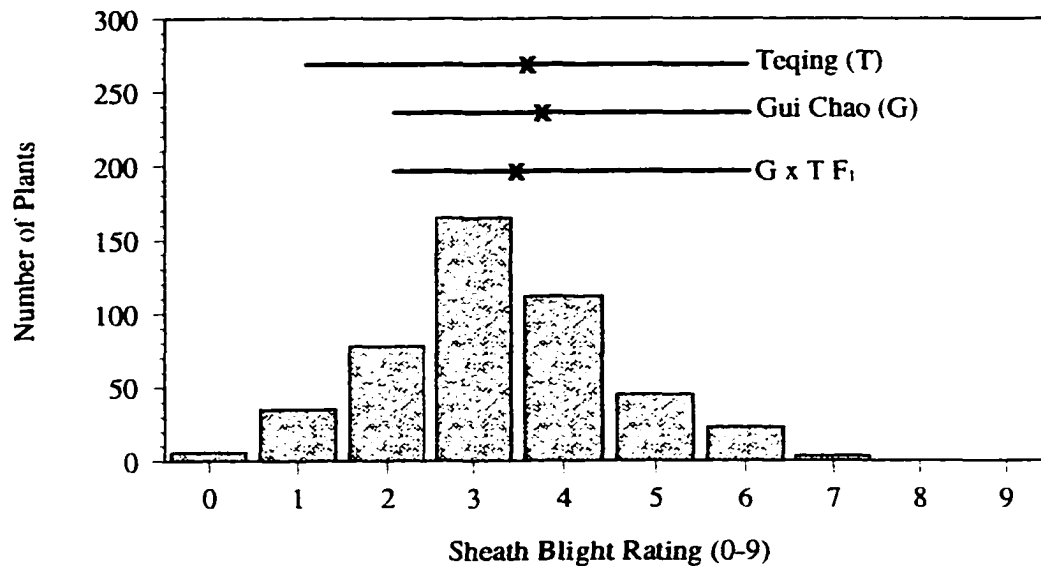


Figure 15. Distribution of sheath blight ratings (0-9) of F₂ plants inoculated by the rice grain/hull method in F₂ populations from a cross between the sheath blight resistant genotypes Gui Chao and Teqing, Crowley, LA, 1996; lines show the rating ranges and x's mark the means for parent and F₁ populations.

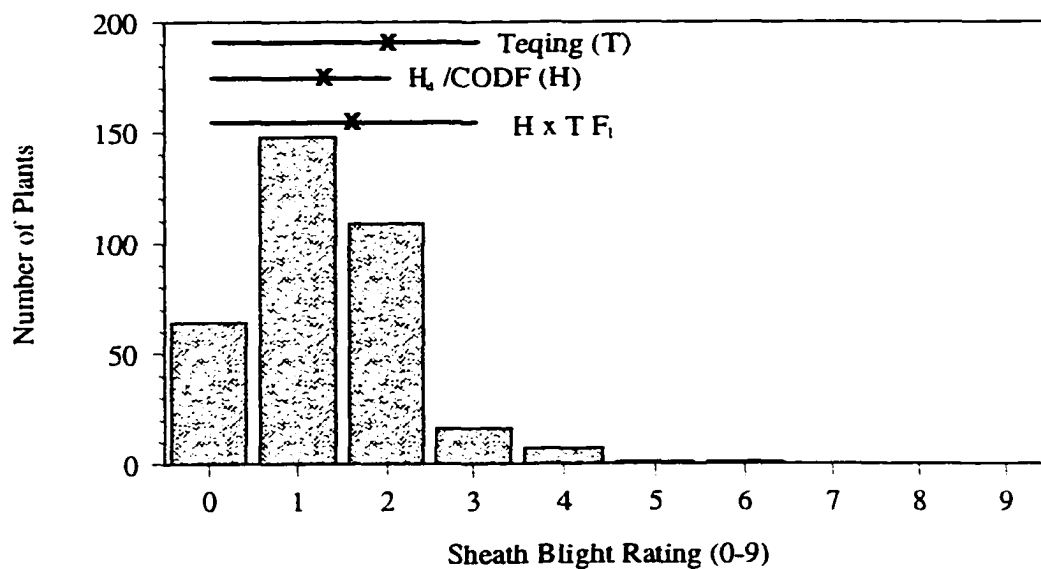


Figure 16. Distribution of sheath blight ratings (0-9) of F₂ plants inoculated by the rice grain/hull method in F₂ populations from a cross between the sheath blight resistant genotypes H₄/CODF and Teqing, Crowley, LA, 1997; lines show the rating ranges and x's mark the means for parent and F₁ populations.

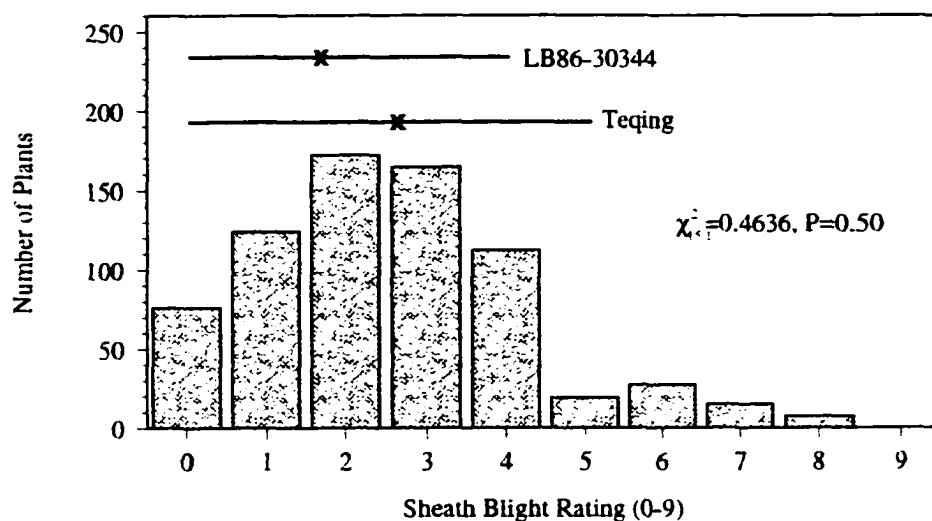


Figure 17. Distribution of sheath blight ratings (0-9) of F_2 plants inoculated by the rice grain/hull method in F_2 populations from a cross between the sheath blight resistant genotypes LB86-30344 and Teqing, Crowley, LA, 1995; lines show the rating ranges and x's mark the means for parent populations.

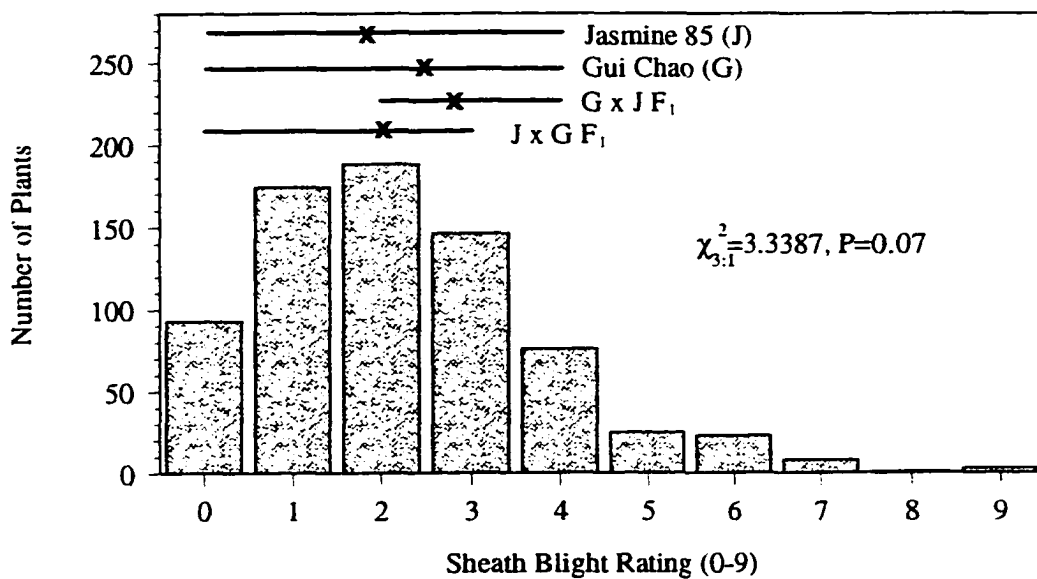


Figure 18. Distribution of sheath blight ratings (0-9) of F_2 plants inoculated by the rice grain/hull method in F_2 populations from a cross between the sheath blight resistant genotypes Jasmine 85 and Gui Chao, Crowley, LA, 1995; lines show the rating ranges and x's mark the means for parent and F_1 populations.

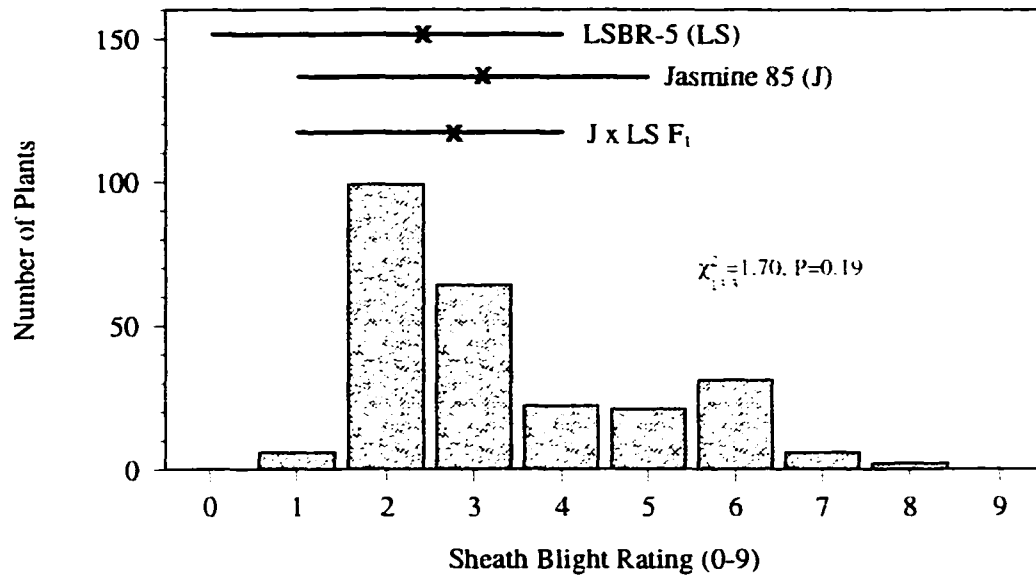


Figure 19. Distribution of sheath blight ratings (0-9) of F_2 plants inoculated by the rice grain/hull method in F_2 populations from a cross between the sheath blight resistant genotypes Jasmine 85 and LSBR-5, Crowley, LA, 1996; lines show the rating ranges and x's mark the means for parent and F_1 populations.

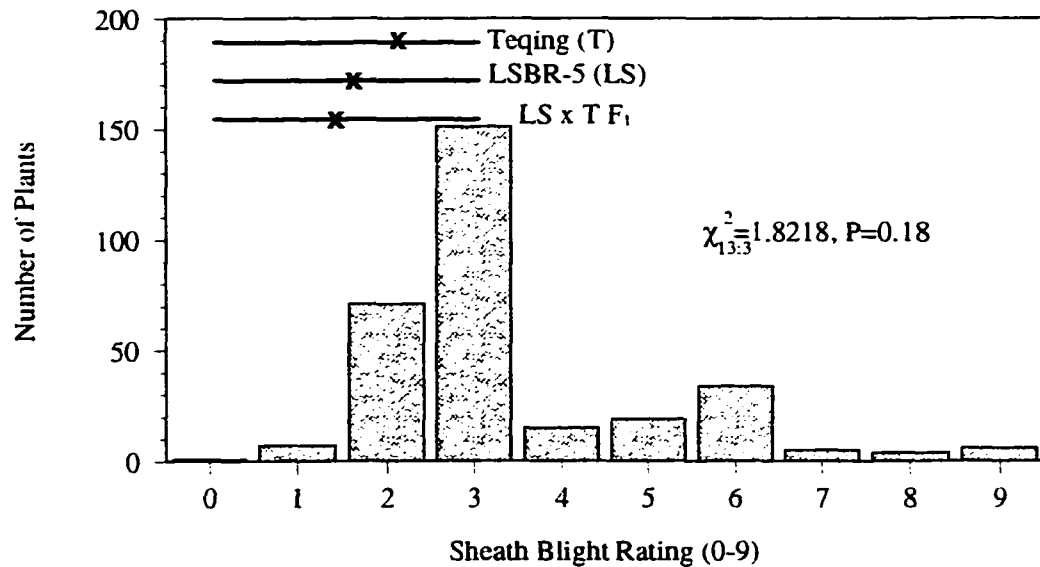


Figure 20. Distribution of sheath blight ratings (0-9) of F_2 plants inoculated by the rice grain/hull method in F_2 populations from a cross between the sheath blight resistant genotypes LSBR-5 and Teqing, Crowley, LA, 1997; lines show the rating ranges and x's mark the means for parent and F_1 populations.

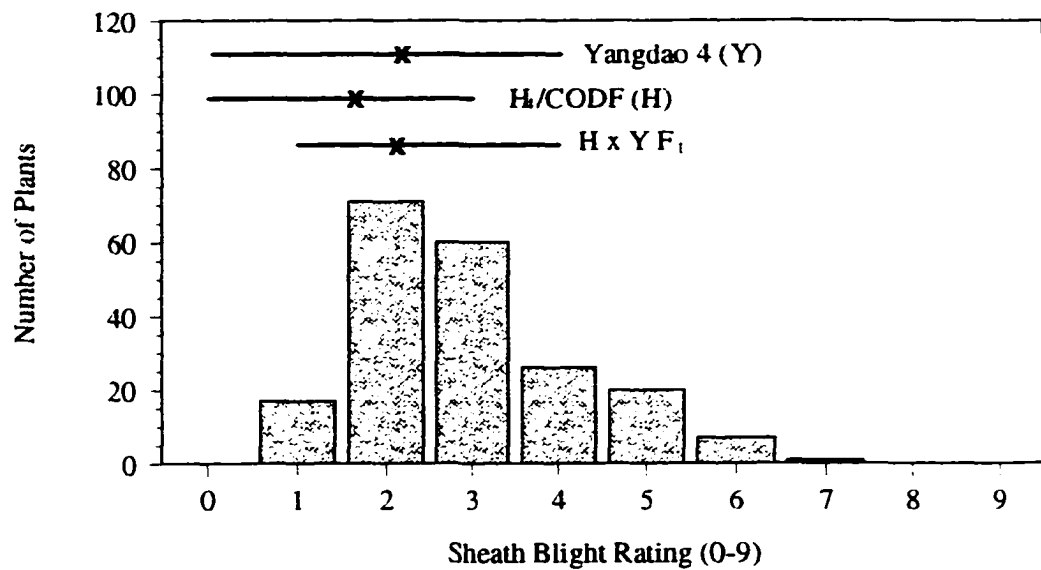


Figure 21. Distribution of sheath blight ratings (0-9) of F₂ plants inoculated by the rice grain/hull method in F₂ populations from a cross between the sheath blight resistant genotypes H₄/CODF and Yangdao 4, Crowley, LA, 1996; lines show the rating ranges and x's mark the means for parent and F₁ populations.

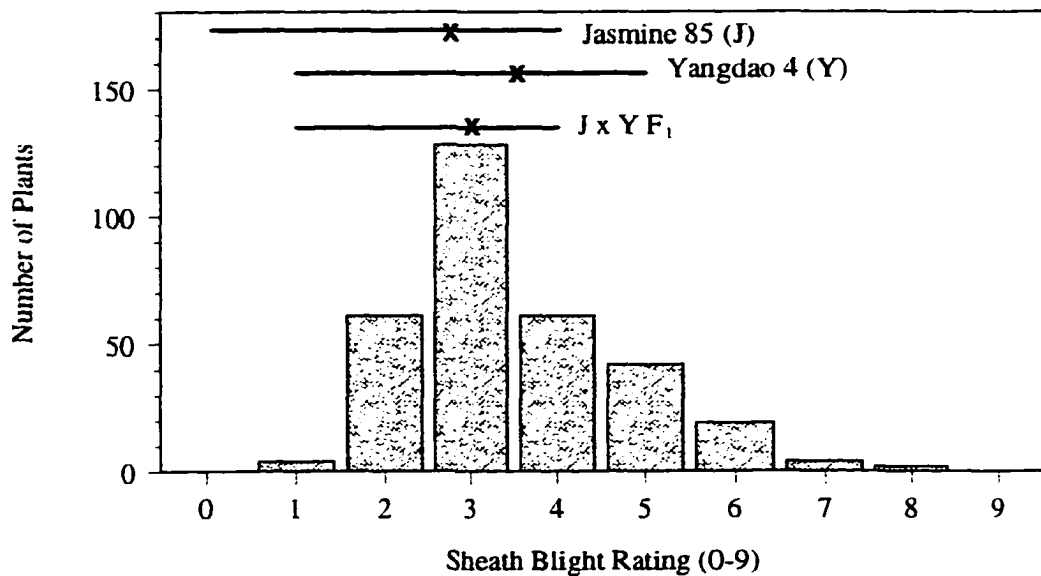


Figure 22. Distribution of sheath blight ratings (0-9) of F₂ plants inoculated by the rice grain/hull method in F₂ populations from a cross between the sheath blight resistant genotypes Jasmine 85 and Yangdao 4, Crowley, LA, 1996; lines show the rating ranges and x's mark the means for parent and F₁ populations.

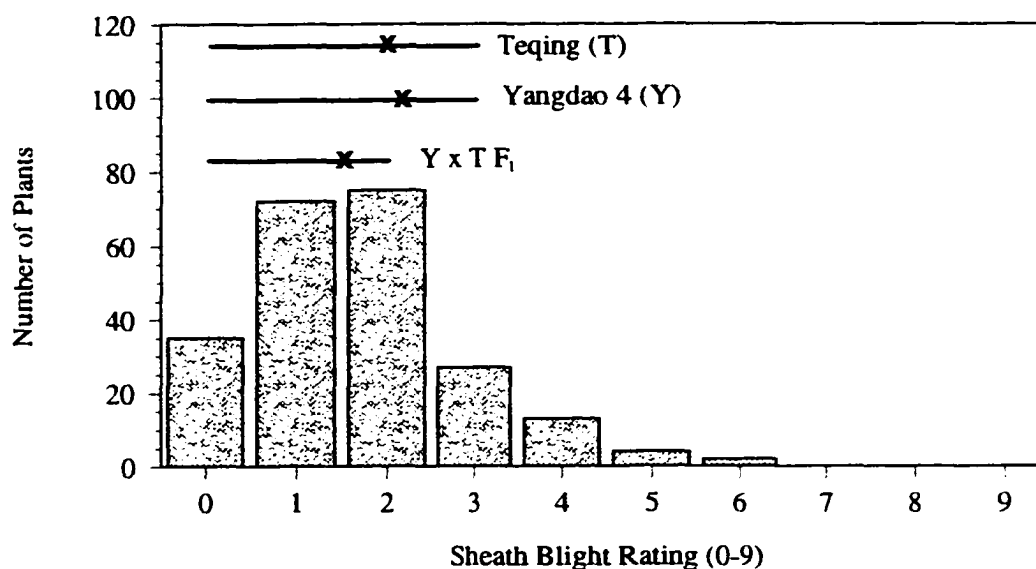


Figure 23. Distribution of sheath blight ratings (0-9) of F₂ plants inoculated by the rice grain/hull method in F₂ populations from a cross between the sheath blight resistant genotypes Teqing and Yangdao 4, Crowley, LA, 1997; lines show the rating ranges and x's mark the means for parent and F₁ populations.

4.3.2. INHERITANCE OF SIMPLE AGRONOMIC TRAITS FROM THE SHEATH BLIGHT RESISTANT PARENTS H₄/CODF AND LB86-30344

All F₁ plants from both reciprocal crosses had the same reddish brown bran color as that H₄/CODF (Table 24). Red pericarp was dominant. Two hundred F₂ plants segregated into 161 red and 39 white, which fit a 3:1 red:white ratio (Table 24). The results from F₁ and F₂ progenies indicated that the red pericarp character of H₄/CODF was controlled by a single dominant gene.

Pubescent foliage is an unacceptable character for the U.S. rice industry. The somaclonal line LB86-30344, derived from the U.S. long-grain commercial cultivar Labelle which has glabrous leaves, has pubescent foliage. All F₁ progenies from reciprocal crosses between LB86-30344 and Lemont also had pubescent foliage. Two

hundred and forty seven F₂ plants segregated into 175 pubescent and 72 glabrous, which fit a 3:1 pubescent:glabrous ratio (Table 25). The results indicated that a single dominant gene conditioned the pubescent foliage character of LB86-30344.

Table 24. Segregation for pericarp color (red or white) among parents and their F₁ and F₂ progenies for the H₄/CODF x Lemont cross, Crowley, LA, 1996.

Rice genotype	Segregation				χ^2	P^b
	Expected ^a		Observed			
	Red	White	Red	White		
Lemont	0	1	0	12	-	-
H ₄ /CODF	1	0	12	0	-	-
H ₄ /CODF x Lemont F ₁	1	0	40	0	-	-
Lemont x H ₄ /CODF F ₁	1	0	23	0	-	-
H ₄ /CODF x Lemont F ₂	3	1	161	39	3.2267	0.07

^a Expected segregation ratio for a single dominant gene

^b Probability that the observed data fit the expected segregation ratio.

Table 25. Segregation for leaf blade pubescence (pubescent or glabrous) among parents and their F₁ and F₂ progenies from the LB86-30344 x Lemont cross, Crowley, LA, 1996.

Rice genotype	Segregation				χ^2	P^b
	Expected ^a		Observed			
	Pubescent	Glabrous	Pubescent	Glabrous		
Lemont	0	1	0	12	-	-
LB86-30344 (LB86)	1	0	12	0	-	-
LB86 x Lemont F ₁	1	0	13	0	-	-
Lemont x LB86 F ₁	1	0	6	0	-	-
LB86 x Lemont F ₂	3	1	175	72	2.2686	0.13

^a Expected segregation ratio for a single dominant gene.

^b Probability that the observed data fit the expected segregation ratio.

Somaclonal line LB86-30344 is tall with a mean plant height of 113.4 cm, while the commercial cultivar Lemont is a semidwarf with a mean height of only 74.5 cm (Table 26). All F₁ plants from reciprocal crosses between these two parents were taller than Lemont, suggesting that tall was dominant to short. The height of F₂ plants from the

LB86-30344 x Lemont cross showed a continuous bimodal distribution. The bottom of the valley between two peaks was at 88 cm. Two hundred and forty seven F₂ plants segregated into 182 tall and 65 short, which fit a 3:1 tall:short ratio. So the dwarf character in Lemont was controlled by a recessive gene, however, the dominant allele for tall was in LB86-30344.

Table 26. Segregation for plant height (tall or short) among parents and their F₁ and F₂ progenies for the LB86-30344 x Lemont cross, Crowley, LA, 1996.

Rice genotype	Mean and range of plant height ^a	Segregation				χ^2	<i>P</i> ^c
		Expected ^b		Observed			
		Tall	Short	Tall	Short		
Lemont	74.5 (69-80)	1	0	12	0	-	-
LB86-30344 (LB86)	113.4 (105-120)	1	0	12	0	-	-
LB86 x Lemont F ₁	117.2 (112-121)	1	0	13	0	-	-
Lemont x LB86 F ₁	116.6 (113-119)	1	0	6	0	-	-
LB86 x Lemont F ₂	102.3 (64-130)	3	1	182	65	0.1099	0.74

^a Plant height in centimeters measured from the plant base to the collar of the flag leaf.

^b Expected segregation ratio for a single dominant gene.

^c Probability that the observed data fit the expected segregation ratio.

4.3.3. LINKAGE ANALYSIS BETWEEN PARTIAL SHEATH BLIGHT RESISTANCE GENES AND GENES CONTROLLING UNFAVORABLE AGRONOMIC TRAITS

Although the six resistant genotypes have major gene controlled partial resistance to ShB, all of them have one or several unfavorable agronomic traits. To transfer partial resistance genes into commercial cultivars without introducing these unfavorable traits, the information on the linkage between the partial ShB resistance and unfavorable traits must be determined. In the previous studies, we already determined that such agronomic traits as tallness, pubescence, and red pericarp were controlled by single genes. The cosegregation of partial ShB resistance along with those agronomic traits were evaluated

on individual F₂ plants for the H₄/CODF x Lemont and LB86-30344 x Lemont crosses. Cosegregation for pericarp color and partial ShB resistance in 200 F₂ plants from the cross H₄/CODF x Lemont did not fit an expected 9:3:3:1 ratio (Table 27), indicating these two genes were linked. However, the crossover value estimated by Allard's method (Allard, 1956) was about 0.45, which means they were loosely linked.

Leaf pubescence and ShB resistance data from 247 individual F₂ plants from the LB86-30344 x Lemont cross data fit the expected cosegregation ratio of 9:3:3:1 ratio with a probability of 0.11 (Table 28). So the gene for pubescent foliage was inherited independently from the gene for partial ShB resistance in LB86-30344.

Cosegregation for partial ShB resistance and dwarfness among F₂ plants from the LB86-30344 x Lemont cross is shown in Table 29. The phenotypes of 247 individual F₂ plants evaluated fit an expected ratio of 9:3:3:1 ratio. Therefore the gene for tallness also was inherited independently from the partial ShB resistant gene in LB86-30344.

Table 27. Cosegregation for partial ShB resistance and red pericarp among F₂ plants from the cross H₄/CODF x Lemont.

R/Rd ^a	R/W	S/Rd	S/W	Total
141	27	27	12	200

^a R=resistant, S=susceptible, Rd=red, and W=white.

$\chi^2_{9:3:3:1} = 10.0089, P=0.02.$

Table 28. Cosegregation for partial ShB resistance and pubescent foliage among F₂ plants from the cross LB86-30344 x Lemont.

R/P ^a	R/G	S/P	S/G	Total
137	58	38	14	247

^a R=resistant, S=susceptible, P=pubescent leaf blade, and G=glabrous leaf blade.

$\chi^2_{9:3:3:1} = 6.060, P=0.11.$

Table 29. Cosegregation for partial ShB resistance and tallness among F₂ plants from the cross LB86-30344 x Lemont.

R/T ^a	R/Sh	S/T	S/Sh	Total
141	54	41	11	247

^a R=resistant, S=susceptible, T=tall, and Sh=short.

$\chi^2_{9:3:3:1} = 3.1916, P=0.36.$

4.4. DISCUSSION

Several studies on the inheritance of partial resistance to ShB have been carried out in Japan and the U.S. Three resistance genes were identified in several resistant materials in Japan, however, their allelic relationship is not known (Hashioka, 1951a, 1951b). Two dominant or partially dominant genes were found to control the partial ShB resistance in Zenith and Caloro, but no allelism information was provided (Masajo, 1976). Greenhouse tests showed that partial ShB resistance in L201 and two breeding lines, RU7902185 and RU7902191, was controlled by two complementary dominant genes, however no crosses between resistant parents were evaluated (Goita, 1985; Hoff et al., 1984; Hoff et al. 1985).

Allelic studies were first carried out on two elite ShB resistant lines LSBR-5 and LSBR-33 developed through somaculture from the ShB susceptible cultivar Labelle (Xie et al., 1990; Xie et al., 1992). LSBR-5 has a recessive gene for partial ShB resistance which is nonallelic to the two recessive genes of LSBR-33. The allelic study carried out by Pan et al. (1995, 1996a, 1996b, and 1998) indicated that the dominant resistance gene in Jasmine 85 was independently inherited from the dominant gene in Teqing. Results obtained in the current study confirmed this conclusion.

The monomodal and normal distribution of disease ratings of the F_2 plants from crosses between resistant parents should be considered an indication of allelic genes existing in two parents. In F_2 populations from the crosses $H_4/CODF \times$ Jasmine 85, Jasmine 85 \times LB86-30344, and Gui Chao \times Teqing, more than 95% of the F_2 plants fell within the range of both parents. The individuals with ratings outside the range of both parents may be showing the effects of minor genes, modifying genes, epistasis, or interaction with environmental factors. No segregation was found in the cross LB86-30344 \times $H_4/CODF$. Apparently, the same or tightly linked genes control the partial ShB resistance in $H_4/CODF$, LB86-30344, and Jasmine 85. The conclusion that both Teqing and Gui Chao have the same gene for partial ShB resistance can also be verified by evaluation of the pedigree of Teqing. In fact, Teqing was selected from a cross between the partially ShB resistant Gui Chao and the susceptible parent TeAn, suggesting that Teqing inherited ShB resistance from its parent Gui Chao (Lin and Ming, 1991).

Bimodal or skewed distribution of disease ratings of the F_2 plants from crosses between resistant parents would indicate that nonallelic genes controlled the partial ShB resistance of the two parents. The bimodal distributions for the crosses Jasmine 85 \times LSBR-5 and LSBR-5 \times Teqing clearly show that the recessive gene in LSBR-5 is nonallelic to the genes in Jasmine 85 and Teqing. This verified that the ShB resistance in LSBR-5 was conveyed by a single recessive gene (Xie et al., 1990, 1992). The bimodal distribution or skewed distribution in the crosses $H_4/CODF \times$ Teqing, LB86-30344 \times Teqing, Jasmine 85 \times Gui Chao showed that the ShB resistance gene in $H_4/CODF$,

LB86-30344, and Jasmine 85 were nonallelic to the gene in Teqing and Gui Chao, which verified the results reported by Pan et al.(1995, 1996a, 1996b, and 1998).

According to the standard procedure for gene nomenclature (FAO International Rice Commission on Nomenclature and Linkage Groups. 1959; Kinoshita, 1985; U.S. Department of Agriculture, ARS, 1963), all the loci for resistance to sheath blight should be designated by *Rh* followed by an Arabic numeral to identify the locus in order of discovery. Alleles at a particular locus would be identified by superscripts. Therefore, the resistance gene in LSBR-5 should be designated as *rh-1*. We are proposing the gene symbol *Rh-2* for the dominant gene which conditions the partial ShB resistance in H₄/CODF, LB86-30344, and Jasmine 85. The locus with dominant alleles for resistance in Teqing and Gui Chao is designated as *Rh-3*.

Both H₄/CODF and LB86-30344 have a high level of partial ShB resistance, but they also have some unfavorable agronomic characters such as red pericarp, tallness, and pubescent leaves. For the efficient use of these resistance sources, it was necessary to determine if these unfavorable agronomic characters were linked with the partial ShB resistance. Although the inheritance of these agronomic traits was determined in many rice germplasms, it was not clear for these two resistant materials (Nagai, 1959; Tsunoda and Takahashi, 1984). The results from this preliminary study showed that all three unfavorable agronomic traits: red pericarp, pubescence, and tallness were found to be single gene controlled. This result was supported by many other studies (Nagai, 1959, Tsunoda and Takahashi, 1984). The pubescence of LB86-30344 may be due to a dominant mutation from somaculture or due to outcrossing. The extreme tallness of

LB86-30344 also may be variation caused by somaculture. Guenzi et al. (1992) reported that a dominant dwarf mutation was derived from a tall plant regenerated from immature wheat embryo derived callus tissue of the hard red winter wheat genotype TAM105.

The analysis of cosegregation between partial ShB resistance genes and the genes for unfavorable agronomic traits showed that the ShB resistance gene *Rh-2*, which conditions the partial ShB resistance in LB86-30344, H₄/CODF, and Jasmine 85, was inherited independently from the genes controlling pubescent foliage and tall plants. However, this resistance gene was loosely linked to the gene for red pericarp, with a crossover value of about 0.45.

From this study, at least three different genes for partial ShB resistance were identified. Pan et al. (1998) reported that two dominant genes *Rh-2* and *Rh-3* had an additive interaction. A large number of resistant breeding lines were developed from the resistance sources LSBR-5, Teqing, and Jasmine 85 (Rush et al., 1995, 1996). It can be predicted that a higher level of partial ShB resistance can be achieved by combining different resistance genes from several sources. The unfavorable agronomic traits, tallness, leaf pubescence, and red pericarp are either not linked or are loosely linked with the ShB resistance gene in Jasmine 85, LB86-30344, and H₄/CODF. So the partial ShB resistance gene could be transferred into commercial cultivars without the risk of introducing those unfavorable traits.

CHAPTER 5. SUMMARY AND CONCLUSIONS

Breeding and releasing resistant varieties is the most practical and economical way to control crop diseases. Although only partial ShB resistance is available, this type of resistance can offer adequate protection against the pathogen under field conditions. To transfer this partial resistance into commercial varieties, a detailed knowledge of the mode-of-inheritance is required. Furthermore, a reliable and efficient procedure for testing progenies of segregating populations has to be developed or selected and utilized.

This study was conducted 1) to compare several published sheath blight inoculation methods and assessment systems with those presently used at Louisiana State University under uniform conditions to select an effective procedure for genetic studies and for breeding for partial ShB resistance, 2) to determine the mode-of-inheritance of partial ShB resistance in six selected resistance sources, and 3) to compare the allelic relationships among the major resistance genes and between the resistance genes and selected genes controlling some unfavorable agronomic traits which were associated with some of those resistance sources.

Four inoculation methods; rice grain/hull mixture (MIX), rice straw (STRW), toothpick (TP), and brown rice (BR), along with five assessment systems; 0-9 rating scale (RAT9), relative lesion height (RLH), disease severity (DS), disease incidence (INCI), and lesion height (LHT) were compared on nine rice genotypes in field tests from 1995 to 1997. The STRW inoculation method induced more than 90% infection on rice tillers, but was unable to separate moderately resistant genotypes from susceptible ones. The BR and TP inoculation methods were unable to induce severe disease on all

genotypes under unfavorable weather conditions. These two methods also were much more time consuming than the MIX method. The best separation between rice genotypes with different levels of partial ShB resistance was obtained by the MIX method of inoculation, which is the procedure presently used by our program at Louisiana State University. This was the most efficient method for identifying true differences in ShB resistance among rice genotypes.

Disease incidence (INCI) assessment was unable to detect differences in ShB resistance among rice genotypes, while lesion height (LHT) failed to differentiate moderately resistant Jasmine 85 from highly susceptible Lemont. The 0-9 rating scale (RAT9), relative lesion height (RLH), and disease severity (DS) assessment systems were generally similar in discriminating among rice genotypes. We have been successfully using the MIX method of inoculation with the RAT9 method of assessment for many years, and it appeared to be the most useful method of inoculation and assessment among all combinations treated.

H₄/CODF, LB86-30344, and Rice/Grass appeared to have ShB resistance mechanisms that inhibit the initial infection by *R. solani* and retard the postinfection development of the fungus. However, Jasmine 85, Gui Chao, and Teqing may only have the mechanism to retard postinfection development.

The inheritance of partial sheath blight resistance was examined in crosses between the resistant rice genotypes H₄/CODF, LB86-30344, Jasmine 85, Teqing, Gui Chao, and Yangdao 4 and the susceptible cultivar Lemont. Parents and F₁, F₂, BC₁F₁, F₃, and F_{2:4} progeny plants were inoculated with the highly virulent *Rhizoctonia solani*

isolate LR172 and evaluated for disease resistance in the field from 1995 to 1997. The results indicated that partial ShB resistance was a dominant character in the sources tested and that maternal effects were not important. Genetic analysis of segregating populations derived from crosses between Lemont and the resistant parents showed that the expected 3:1 resistant:susceptible ratio in F_2 generations, characteristic of a character controlled by a single dominant gene, were found for crosses with all parents except for Yangdao 4, and were confirmed by evaluation of F_3 or $F_{2,4}$ lines and BC_1F_1 populations. Therefore, H₄/CODF, LB86-30344, Jasmine 85, Teqing, and Gui Chao each appear to have one dominant gene controlling most of their partial resistance to sheath blight. This was considered to be major gene resistance because resistant plants were readily identified in the segregating populations. Plants in F_2 populations from the crosses between Yangdao 4 and Lemont segregated in a 9:7 resistant:susceptible ratio, which indicated that two complementary dominant genes may control the partial ShB resistance in Yangdao 4. Major gene effects were estimated to be 2.7 and 4.8 rating scale points, depending on the specific F_2 population and resistance source.

Strong correlations were observed between F_3 and $F_{2,4}$ lines for partial ShB resistance from the crosses Jasmine 85 x Lemont, Teqing x Lemont, and LB86-30344 x Lemont. Significant correlations also were found between F_2 and F_3 lines, and between F_2 and $F_{2,4}$ lines for all crosses except for Teqing x Lemont. These results provide further evidence that partial ShB resistance was a heritable characteristic. The broad-sense heritabilities estimated using the variance components obtained from the analyses of variance of disease ratings of the F_3 and $F_{2,4}$ lines from Jasmine 85 x Lemont were 73.2%

and 79.3%, respectively. For the LB86-30344 x Lemont cross, the broad-sense heritabilities estimated using the F_3 and $F_{2,4}$ lines were 74.0% and 82.1%, respectively. The high broad-sense heritability coupled with the bimodal distribution of ShB ratings for F_2 plants, was a strong indication of major gene resistance.

Crosses were made among seven sheath blight resistant genotypes to evaluate the allelic relationships of their ShB resistance genes. Two additional crosses between the sheath blight resistant rice genotypes H₄/CODF and LB86-30344 and the susceptible variety Lemont also were tested for possible linkages between the ShB resistance gene and the genes for unfavorable agronomic traits.

The results from allelic studies showed that no segregation for susceptible F_2 plants was observed for the crosses among H₄/CODF, LB86-30344, and Jasmine 85. All F_3 lines from the LB86-30344 x H₄/CODF cross were homogeneous resistant. These results suggested that the single dominant genes in these three genotypes were the same or tightly linked. This gene was designated as *Rh-2*. All F_2 plants from the Gui Chao x Teqing cross had a disease reaction similar to that of both parents, indicating that Gui Chao and Teqing had the same gene for resistance which was designated as *Rh-3*. Susceptible F_2 plants were observed from the crosses between the genotype group of H₄/CODF, LB86-30344, and Jasmine 85, and the genotype group of Teqing and Gui Chao. The data from some crosses fit a 15:1 resistant:susceptible ratio, which indicated that *Rh-2* and *Rh-3* assorted independently from each other. F_2 plants from the Jasmine 85 x LSBR-5 and LSBR-5 x Teqing crosses segregated in a 13:3 resistant:susceptible ratio, indicating that the recessive gene in LSBR-5, designated as *rh-1*, was inherited

independently from both *Rh-2* and *Rh-3*. Both dominant ShB resistance genes in Yangdao 4 were different from *Rh-2* and *Rh-3*, however, the linkage was not tested due to the small F₂ population size. The transgressive segregation for ShB resistance observed in most of the crosses among the resistance sources indicated that the major genes *Rh-2* and *Rh-3* may have additive effects.

Three undesirable agronomic traits; tall plants, red pericarp, and pubescent foliage, in some of the six resistant parents were found to be monogenically inherited. The ShB resistance gene *Rh-2* was inherited independently from the genes controlling plant tallness and pubescence, but was loosely linked to the gene for red pericarp with a crossover value around 0.45.

Results from this research clearly indicated that most of the partial ShB resistance in a cultivar or line may be controlled by one or two genes that are either dominant or recessive. Resistant progenies can be identified from segregating populations from the crosses between resistance sources and susceptible varieties. We believe that this partial resistance should be considered major gene resistance. The findings of this research should accelerate the ongoing breeding effort for sheath blight resistance.

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VITA

Xueyan Sha was born on January 12, 1964, in Jiang Jia Gang city, Jiangsu Province, China. He received his secondary education from Hu Chao Gang Middle School in Jiangsu Province, China. In the fall of 1980, he entered Nanjing Agricultural University in Nanjing, China, majoring in Agronomy. He received his bachelor's degree in the summer of 1984, and his master's degree in Plant Genetics and Breeding in 1987. He was a research associate in the Department of Agronomy, Nanjing Agricultural University, from 1987 until 1990, when he was promoted to Lecturer. He was assigned to the rice genetics and breeding for disease resistance projects within the University. In June of 1994, he enrolled at Louisiana State University to pursue a doctoral degree under the guidance of Dr. M. C. Rush and Dr. S. D. Linscombe. He is a member of the American Phytopathological Society, the Southern Division of the American Phytopathological Society, the Louisiana Plant Protection Association, and serves as a student representative on the Departmental Safety Committee. He is now a candidate for the degree of Doctor of Philosophy in Plant Health, which will be granted in December, 1998.

DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: Xueyan Sha

Major Field: Plant Health

Title of Dissertation: Measurement and Inheritance of Resistance to Sheath
Blight Caused by Rhizoctonia solani Kuhn in Rice

Approved:

Milton C. Rush
Major Professor and Chairman

John M. Kerlin
Dean of the Graduate School

EXAMINING COMMITTEE:

Sh. L. L. L.
Co-Chairman

James D. D.

Richard C. L.

Jeffrey V. H.

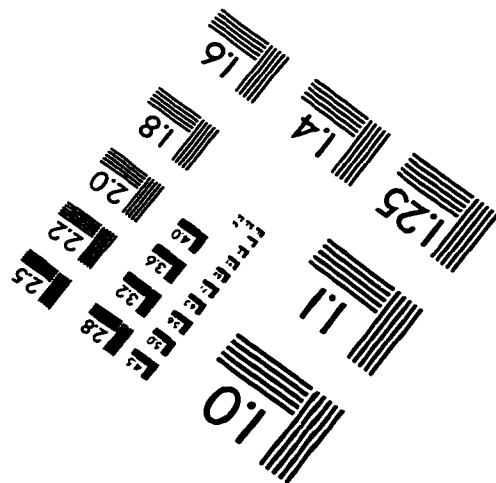
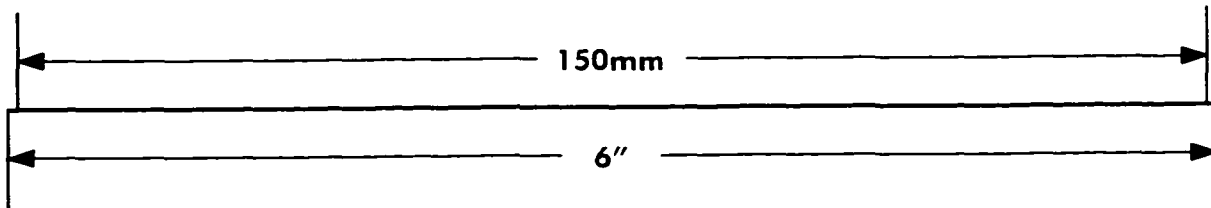
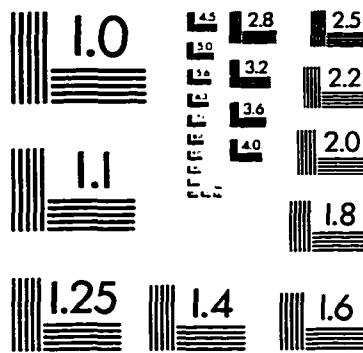
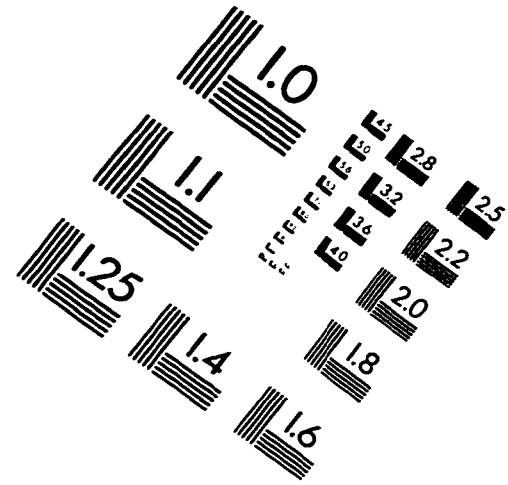
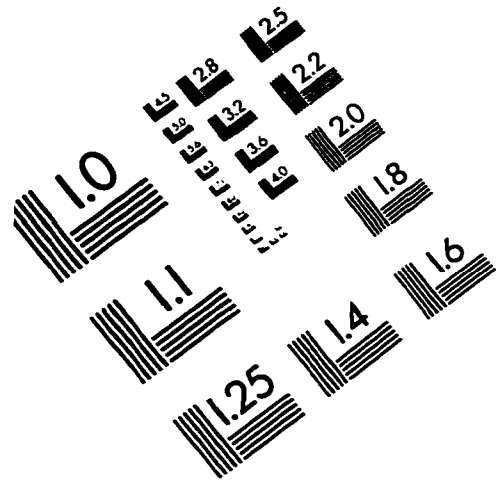
John S. M.

D. D. D.

Date of Examination:

July 10, 1998

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